LATE PLEISTOCENE COLD-BLOODED VERTEBRATE FAUNAS FROM THE MID-CONTINENTAL UNITED STATES

I. Reptilia; Testudines, Crocodilia

Robert E, Preston

Claude W. Hibbard Memorial Volume 6

1979

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Museum of Paleontology The University of Michigan Ann Arbor, Michigan 48109

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I. Reptilia; Testudines, Crocodilia.

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ABSTRACT

Local faunas containing fossils of turtles and alligators and located principally in the Great Plains and Central Lowlands physiographic provinces (Fenneman, 1931) are reviewed. A temporal sequence is outlined for these faunas based on published information regarding stratigraphy, faunal shifts and radiogenic dates, as well as on new data available from the study of reptiles and amphibians. An attempt is made to determine the dates of extinction or major faunal shifts in various areas. In general this can be done only on a relative basis; however, it appears that the small tortoise, Hesperotestudo wilsoni, became extinct and Terrapene carolina, forest box turtles, disappeared from New Mexico and western Texas after the time of the Llano culture (Clovis points), but by the time of Folsom occupation at Lubbock Lake (i.e., between 11,000 and 10,000 years ago). The time of extinction of Gopherus and large Hesperotestudo has not been determined. Comparison of chelonian faunal compositions between the interval under discussion and both earlier fossil assemblages and the Recent faunas indicate a gradual southward and/or eastward contraction of ranges of some forms in northern Nebraska. Similar contractions are evident in Kansas, along with possibly sporadic invasions of species with primarily more southern or eastern distributions. In Texas distributional events are well known only for the past 50,000 years or so, but display similar patterns as well as minor fluctuations of ranges over small time intervals. In general the most dramatic changes in faunal composition occur during and at the close of Wisconsinan glaciation. The importance as indicators of climate and local habitat of the reptiles, amphibians and fishes of each local fauna is discussed.

Numerous new faunal and geographic records for turtles in the late Pleistocene are presented. Occurrences of Graptemys pseudogeographica and floridana-group Chrysemys are documented for the Great Plains. A new species, Chrysemys hibbardi, making singular appearances in two local faunas of similar composition, is described. Detailed characters for systematic placement of shell bones belonging to the genus Chrysemys are presented. Chrysemys timida Hay is considered synonymous with C. picta. Pseudemys bisornatus Cope and Emys petrolei Leidy are maintained in synonymy with Chrysemys scripta. The portion of the type-specimen of Trachemys trulla Hay that belongs to this subgenus (in current usage) is also referred to Chrysemys scripta. All material considered in this paper belonging in the genus Gopherus is referred to a single, possibly undescribed, probably extinct species. Material referable to Hesperotestudo (Williams, 1950b; Geochelone of most authors) is divided among two described species and two additional uncertain or undescribed specific placements. A key to aid in identification of late Pliocene-Recent fossil turtle-shell bones of the eastern and central United States and Canada is presented as an appendix.

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INTRODUCTION

Depositional cycles during the ice age have left a seemingly endless but potentially extremely detailed sequence of fossil-bearing sediments in the central United States and adjacent Canada and Mexico. In addition to those from stream and river terrace deposits, which can sometimes be traced over reasonably large geographic areas, fossil biotas are obtained from isolated lake deposits and small fillings of local collapse basins as well as from caves in regions where these occur.

The majority of the deposits are outside the limits of continental glaciation and, in all cases, correlations with sequences of till, soil and loess in formerly-glaciated North America are difficult. Recently developed methods of refined faunal analysis, magnetic geochronology, and radiometric dating of volcanics and carbonaceous remains, have made time-correlation with the depositional sequence in glaciated regions a possibility. More importantly, however, the chronology of the nonglaciated areas, which are not only vast in geographic extent but also inherently rich and varied in biotic composition, can be broken down into intervals of relatively short duration with absolute dates available for their boundaries and, in the case of datable remains, for individual events.

The stretch of time leading up to and including the catastrophic events at the close of the Pleistocene is one for which a large accumulation of faunistic and floristic data is available. This interval is also generally considered important in contributing to an understanding of distributions of animals and plants within and between the biotic regions of Recent North America. The fission-track age of 0.6×10^6 years for the last-known wide-spread deposit of a Pearlette volcanic ash on the Plains provides a convenient point of departure for the selection of faunas to be discussed in this paper. A currently suitable date for the Plio-Pleistocene boundary in the Plains has been given as approximately 1.8×10^6 years ago (see Zakrzewski, 1975). So-called "long chronologies" favor even earlier dates. Accordingly,

the period under consideration here is, at most, the last third of the Pleistocene, hence the choice of the designation late Pleistocene. This period is entirely within the Brunhes interval of normal magnetic polarity with respect to the present (Lindsay *et al.*, 1975). Except for the Arkalon and Kanopolis, and probably the Slaton, Rezabek and Berends local faunas, the period is restricted to the Rancholabrean land-mammal age.

Hibbard and Taylor (1960; also Hibbard, 1970, p. 397) have stressed the unusually sensitive nature of the Great Plains region with respect to its ability to reflect distributional shifts due to climatic change. The sequence of faunas from Texas reviewed in this report is capable of documenting not only major changes in distributions in the southern Plains and Plateau divisions of this area, but, in addition, fluctuations in a formerly more widespread Gulf Coast biota. Detail is indeed sufficient to depict changes in the boundaries of biotic regions as delineated for the Recent fauna of Texas.

Intensive study during recent years of late Pleistocene fossil vertebrates in the central United States has been championed largely by C. W. Hibbard (Kansas and adjacent Oklahoma), C. B. Schultz, T. M. Stout and L. G. Tanner (Nebraska), W. W. Dalquest, E. L. Lundelius and B. H. Slaughter (Texas), and P. W. Parmalee (Mississippi Valley states), among others. Forty years of collecting in central and southwestern Kansas and nearby Oklahoma, augmented by the washing technique described by Hibbard (1949), has resulted in the publication of several doctoral dissertations (e.g., Stephens, 1960; Schultz, 1965; Semken, 1966) concerned with the stratigraphy and vertebrate paleontology of individual deposits. In addition, this work has culminated in the appearance of synoptic treatments by Hibbard and Taylor (1960, vertebrates and molluscs), Kapp (1965, the pollen record) and Miller (1966, molluscs) of important sequences of fossil biotas. In the spring of 1967, Professor Hibbard and students at the University of Michigan conducted a seminar on late Pliocene and Pleistocene faunas and climates. One result was a tabulation and discussion of mammalian local faunas of the Great Plains and Central Lowland physiographic provinces by Hibbard (1970). It was the hope to publish a compilation of all known vertebrates from these localities at that time but, in the area of reptiles and amphibians particularly, cataloging and description were incomplete.

I have had the privilege of studying the fossil turtle collection in the University of Michigan Museum of Paleontology for several years and have visited some of the late Pleistocene localities in southwestern Kansas. I have also been able to look at additional material at the Universities of Kansas and Nebraska. Identification and cataloging of turtle specimens is now up to date. The tabulation of this material will, in part, extend the invaluable annotated bibliographies compiled by Gehlbach (1965) and Holman (1969b). In addition to these bibliographies and the work of O. P. Hay earlier in the century. I have relied upon the numerous treatments of faunal segments and individual taxonomic groups cited below in the review of local faunas. Several other essays and reviews, for example those of Auffenberg and Milstead (1965), R. R. Miller (1965) and Cross (1970) have contributed ideas.

I have attempted to give complete citations of the herpetological and ichthyological references for each of the fossil localities discussed herein. Part II of this survey, which is now in preparation, will review the remainder of late Pleistocene localities, *e.g.*, the central-Texas faunas discussed by Lundelius (1967), for which herpetological and ichthyological records exist, and will present listings of the fishes, amphibians and squamate reptiles for all the localities.

Abbreviations

Terms, units:

cf.	(best) compared with, closest comparison to
С.М.	Central Meridian
fm	formation
km	kilometers
KU Loc.	University of Kansas Meade Co. locality
1.b.	local biota
1.f.	local fauna
m	meters
Sec., T, R	section, township, range
sp.	species

Terms, units:

UM-K.	University	of Michigan	Kansas locality
		1 0	,

yr. years ago, years before present

All measurements are given in millimeters.

Specimen catalog numbers:

AMNH	American Museum of Natural History				
ANSP	Academy of Natural Sciences, Philadelphia				
FMNH	Field Museum of Natural History				
KU	University of Kansas Museum of Natural History				
MSU	Michigan State University Museum				
NMNH	National Museum of Natural History, Smithsonian Institution				
PPHM	Panhandle-Plains Historical Museum				
PU	Museum of Natural History, Princeton University				
SUI	State University of Iowa				
SMUMP	Schuler Museum of Paleontology, Southern Methodist University				
TMM	Texas Memorial Museum, University of Texas at Austin				
UM	University of Michigan Museum of Pale- ontology				
UMMZ	University of Michigan Museum of Zoology				
UNSM	University of Nebraska State Museum				
UT	Skeletal collection, University of Texas				
V-	UM Vertebrate				
WAA	Collection of William A. Akersten				

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SEQUENCE OF LOCAL FAUNAS

Pliocene – early Pleistocene background.- Tortoises are the conspicuous chelonian representatives of later Blancan (?early Pleistocene) local faunas; those that include aquatic forms are comparatively few in number. The Sand Draw 1.f., Brown Co., Nebraska (Holman, 1972a) and the White Rock 1.f., Republic Co., Kansas (Eshelman, 1975) together with records from the Crooked Creek and Ballard formations of southwestern Kansas (Preston, in preparation A) have yielded the following composite turtle fauna:

Kinosternon flavescens, yellow mud turtle

Trionyx sp., softshell

Chelydra serpentina, snapper

Terrapene ornata, ornate box turtle

Chrysemys (Chrysemys) picta, painted turtle

Chrysemys (Trachemys) scripta, pond slider

Hesperotestudo sp., turgida group, smaller tortoises Hesperotestudo cf. H. campester, giant tortoise Gopherus sp. gopher tortoise

The two *Hesperotestudo* lineages and *Gopherus* are represented in the Blancan faunas of Texas as well. *Kinosternon* is recorded from the Blancan Benson 1.f. of Arizona but so far is unreported from the Pleistocene of Texas prior to the Folsom horizon at Lubbock Lake. *Chelydra* has been found only in the White Rock 1.f.

Rexroadian (Kúrten, 1971; ?latest Hemphillian – early Blancan) faunas from Kansas and their presumed equivalents in Texas turn out to have had essentially the same generic composition as the later Blancan with the addition of *Macroclemys temmincki* (Hibbard, 1963a), *Emydoidea* (Preston and McCoy, 1971) and *Graptemys* cf. *G. geographica* (Preston, in preparation B). *Chelydra* is common. *Sternotherus* and, possibly, the *carolina* group of box turtles are present in the early Pliocene of Kansas (Holman, 1975), but as far as now known these forms do not reappear in the Great Plains until the late Pleistocene. Extant species of the subgenus *Chrysemys (Pseudemys)* apparently entered the region only in the late Pleistocene. *Kinosternon* cf. subrubrum (Fichter, 1969; Saw Rock Canyon l.f.) and *Macroclemys* have not been found in Pleistocene faunas in the central United States, with the possible exception of the latter species. A well-mineralized specimen was dredged from the Brazos River near College Station, Texas, but Hay (1911) considered it as being of Holocene age.

The earlier Irvingtonian faunas (see Hibbard, 1970; Hibbard and Dalquest, 1973) probably have roughly the composition outlined in the above list. I thought Chelydra and Kinosternon were absent from the Gilliland l.f., Knox and Baylor Co.'s, Texas, due to unsuitable habitat (Preston, 1966). Kinosternon is represented in the Borchers l.f., Meade Co., Kansas, but so far Chelydra has eluded notice (Preston, in preparation A). The Trionyx in the Gilliland 1.f. is identifiable as T. spinifer and the box turtle is referable to T. ornata ornata. Chrysemys (Trachemys) scripta compares best with the Recent subspecies C. s. elegans. Chrysemys picta occurs in the Gilliland 1.f. (Preston, in preparation A). Alligator is found in the Gilliland 1.f. as well as in the Beck Ranch l.f. from the early Blancan of Scurry Co., Texas (Rogers, 1976).

The Cudahy fauna (see Hibbard, 1970), which occurs over a wide geographic area directly beneath the Pearlette (restricted to type "O", Boellstoerff, 1973; Naeser *et al.*, 1973) volcanic ash, would be the ideal starting place for a discussion of late Pleistocene faunas. Unfortunately, the number of turtle species represented in this and other faunas thought to represent glacial maxima is typically low. Whether this phenomenon is due to circumstances of deposition or is a true indication of a depauperate fauna is not known. In any case I know of only one species (*Chrysemys picta*) in any Cudahy fauna (Preston, in preparation A).

The Arkalon l.f. of Seward Co., Kansas, is apparently closely associated with one of the depositions of Pearlette-type volcanic ash. Pure ash has not been available for dating in recent years, but it is hoped that a lens may eventually be exposed for this purpose. However, the muskrat recovered from this locality is assignable to Ondatra annectens, the form associated with Cudahy local faunas (Semken, 1966; Hibbard and Dalquest, 1973). This suggests an age similar to that of the Cudahy and indicates that the ash should be type "O", from 0.6×10^6 yr. Nine species of turtles occur in the Arkalon 1.f. Except for the presence of Chrysemys floridana and turgida-line Hesperotestudo, it contains forms commonly found in younger deposits up to the time of Wisconsinan glaciation in southwestern Kansas.

Annotated list of late-Pleistocene local faunas.- These faunas (or biotas) are outlined in Figure 1 on the basis of known or implied stratigraphic succession. Previous errors in assignment of relative age will be perpetuated and, undoubtedly, new ones will be introduced, but some sort of logical framework is necessary to bind together a discussion of thirty-odd localities. Figure 1 also shows the approximate limits of glacial or interglacial stages to which the faunas have been assigned by most authors. Potentially significant stratigraphic markers are indicated for the Meade Co., Kansas (Kapp, 1965; G. E. Schultz, 1969) and Nebraska (C. B. Schultz and Martin, 1970) regions. Some microevolutionary data and zoogeographic events implied by this hypothetical succession are also shown.

The geographic setting of the faunas from Nebraska, Kansas and the Oklahoma panhandle are shown in Figure 2. Localities in Texas (Fig. 3) which I regard as providing good representations of turtle faunas are the Clear Creek 1.f. (star), Ingleside 1.f. (circle), Pitt Bridge localities (triangle), Berclair Terrace (diamond) and the Lubbock Lake site (square). The locations of less-representative local faunas and isolated records are indicated by the species recovered (see legend, Fig. 3). Selected faunal compositions (turtles and crocodilians) are shown in Table 1, with the Recent fauna of the corresponding areas presented for comparison. For each local fauna in the following list and those localities mentioned only in Figure 3, I have cited the original or most complete faunal discussion in previous literature and/or the source for a complete bibliography of the fauna, and all articles dealing with herpetological and ichthyological aspects.

Central and Southwestern Kansas, Oklahoma Panhandle

Arkalon 1.f. W¹/₂ Sec. 35, T 33 S, R 32 W, Seward Co., Kansas (Hibbard, 1953; Preston, 1971). Figs. 1, 2(1); Table 1. The stratigraphic position and faunal affinities of this local fauna were mentioned above. No matrix has been washed from this locality, and the squamate reptile, amphibian and fish segments of the fauna are Additional collecting would be desirable unknown. to lend more credibility to the apparent absence of Kinosternon, Terrapene carolina, and large Hesperotestudo. The first record of Emvdoidea since the late Pliocene appears in the Arkalon 1.f. Two specimens of a small member of the Chrysemys (Pseudemys) floridana group have been collected. They signify the earliest known appearance of a representative of this subgenus in the Plains that is referable to a Recent species (cf. C. floridana hoyi). This species is not seen again in fossil faunas, but it and races of the closely related species, C. concinna, occur now in eastern Kansas and Oklahoma (Fig. 2) and across Texas to the Pecos River (Conant, 1975, maps 23, 24). The Arkalon l.f. is the youngest Great Plains assemblage containing abundant remains of the extinct tortoise (Hesperotestudo, sp. "B") belonging to the *turgida* series originally defined by Auffenberg (1963).

In my discussion (Preston, 1971) of the local habitat (lake, pond, or slow-moving stream) I failed to stress the fact that most of the specimens of aquatic turtles are associated fragments of partially- or nearly-complete shells. Thus, the depositional site itself provided the habitat (silt bottom, abundant vegetation) preferred by these species, which is in agreement with Hibbard's (1953) conclusions from the lithology at the site. Hibbard (1970) mentioned potential similarities in faunal composition between the Arkalon 1.f. and the Rock Creek 1.f. of Briscoe Co., Texas.

Kanopolis 1.f. SW¼ NE¼ Sec. 25, T 15 S, R 8 W, Ellsworth Co., Kansas (Holman, 1972b; Neff, 1975; Hibbard *et al.*, 1978). Figs. 1, 2(2); Table 1. Hibbard and Dalquest (1973) group the Kanopolis, Rezabek and Slaton local faunas in the same time interval based on the occurrence of the water rat, *Neofiber*, which Hibbard (1970) regards as having had a less restricted distribution during this period than at present due to availability of suitable marshy habitats. The muskrats in the Kanopolis and Rezabek local faunas are assigned to *Ondatra nebrascensis* (Hibbard *et al.*, 1978).

The fish fauna (Neff, 1975), evidently the most complete of late-Pleistocene fish assemblages reported to date, is composed of both small stream and low- to base-gradient river communities. The comparable Recent area of sympatry lies to the east of Ellsworth Co. (The



Figure 1. Sequence-outline of local faunas discussed in the text, with approximate radiometric dates, Pleistocene stage assignments and selected stratigraphic indicators included for comparison. Potentially important faunal-compositional and biostratigraphic information is also shown.

area of sympatry is defined as that region in which Recent populations of all or most of the species known from the fossil fauna occur together. Under the assumption of identical physiological requirements for fossil and Recent individuals assigned to the same species, the area of sympatry indicates the habitat, and presumably the contributing climatic conditions, in the vicinity of the fossil locality at the time of deposition.) This determination is made independently on the basis of either the fishes or the reptiles and amphibians (Holman, 1972b) although some of the differences between the fish distribution at the time of deposition and now are thought to be due to changes in drainage patterns. Drainage of the ancestral upper Smokey Hill River directly into the Arkansas system at some time prior to the Kanopolis interval has been documented. and the possibility of southward drainage through the Cottonwood-Neosho system at the time of the Kanopolis has been suggested (see B. B. Miller, 1970, and Neff, 1975).

The western limit of Recent Graptemys geographica occurs to the east of Ellsworth Co., as do the western distributional boundaries of Sternotherus and Chrysemys (Pseudemys) concinna at this latitude.

There is a tortoise in the fauna, but I have been unable to identify it with absolute certainty. The entry "Geochelone sp.", added in proof to Holman's (1972b) list of Kanopolis reptiles and amphibians, is based on a worn fragment of shell (V-61007) which was probably reworked from earlier sediments. I have assigned the material described in the Systematics section to Hesperotestudo cf. sp. A (larger tortoise) but there is a possibility it might, instead, represent Gopherus.

Rezabek l.f. Gravel pit, Sec. 20, T 13 S, R 10 W, Lincoln Co., Kansas. KU Lincoln Co. Loc. 5 (Hibbard, 1943; Brattstrom, 1967; Lundberg, 1975). Figs. 1, 2(3). Hibbard and Dalquest (1973) considered this the youngest of the three local faunas (Slaton, Kanopolis, Rezabek) containing Neofiber. A cooling trend is evidenced by some mammalian species (e.g., large Blarina, Sorex cinereus, and Microtus pennsylvanicus). According to Hibbard (1943) fish remains, including Lepisosteus, ictalurids and centrarchids, are abundant. Numerous amphibians were also collected but apparently have not been studied. The only snake mentioned by Brattstrom (1967) is Natrix cf. N. sipedon. The turtles consist of Kinosternon flavescens, Chelydra serpentina and Chrysemys picta.

Berends 1.b. NW¼ Sec. 8, T 5 N, R 28 E(C.M.), Beaver Co., Oklahoma (Miller, 1966; Hibbard, 1970; Brattstrom, 1967; C. L. Smith, 1954, 1958; Preston and McCoy, 1971; Lundberg, 1975). Figs. 1, 2(4); Table 1. Miller (1966) considers the Berends the oldest among a sequence of five faunas presumably associated with phases of Illinoian glaciation. Two molluscan species in this assemblage do not reappear in the remainder of the sequence, and one of them, Planorbula armigera, a species of presently eastern distribution, appears to have become locally extinct after the time of the Berends biota. Kapp (1965) finds the pollen spectrum to contain high percentages of spruce and pine, and similar to that of the stratigraphically lowest horizons at the Doby Springs (locality 5 of Stephens, 1960) and Butler Spring (Adams 1.f.) localities. The best correlation with these biotas is offered by the upper part of the Berends section, from which the fossils are derived, although samples from the entire 10 meters of exposed sequence indicate stability of the relatively cool, moist climatic conditions implied by the species present.

The fish fauna, represented thus far by twelve taxa, contains some species of presently northern distribution, *Esox masquinongy* and *Perca flavescens*. Mammals in this category include *Sorex cinereus*, larger *Blarina*, and *Microtus pennsylvanicus*, all shared by the Rezabek and many of the following local faunas currently placed in the Illinoian interval.

The large quantity of turtle remains have been termed "unidentifiable" in previous publications. Nine taxa are readily identified (Table 1), three of which, K. flavescens, Emydoidea, and Chrysemys picta are represented by numerous bones. Although associated parts from single individuals were not found, these three species probably lived at the depositional site, which Hibbard and Taylor (1960) believed to be a large embayment of the ancestral Cimarron River. Chelydra and Trionyx are also well represented, although by fragmentary specimens. Only one bone each are identifiable as Sternotherus and Chrysemys scripta. The terrestrial forms Terrapene ornata and Hesperotestudo are poorly represented. The Recent distributions of three of the extant members of the fauna, K. flavescens, S. odoratus and C. (Trachemys) scripta, are considerably to the south or east of the area of sympatry (northeastern Nebraska-northwestern Iowa) deduced by Miller (1966) for the molluscan fauna.

R. E. PRESTON: LATE PLEISTOCENE TURTLES AND ALLIGATORS

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	TESTUDINES	Kinosternidae Kinosternon flavescens Sternotherus odoratus	Trionychidae Trionym spinifer Musical spinifer	Chelydra serpentina	Terrapene, carolina group Terrapene ormata	Graptemys geograptica Graptemys pseudogeogr./kohni Chrysemys picta	iracnemys scripta Pseudemys, floridana group ?Pseudemys hibbardi	Emydoidea blandingi Testudinidae	coprerus sp. Hesperotestudo, sp. "A" Hesperotestudo, sp. "B"	CROCODILIA	Crocodylidae <i>Alligator</i> sp.	NOTES	¹ Restricted to Stephens' (1960) ² Part of the Mt. Scott local fe	³ These localities constitute th (Schultz, 1969)

TABLE 1.

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Doby Springs 1.b. N¹/₂ SW¹/₄ Sec. 10, T 27 N, R 24 W, Harper Co., Oklahoma (Miller, 1966; Hibbard, 1970; Brattstrom, 1967; Etheridge, 1960a, 1961; Preston and McCov, 1971; Smith, 1958; Tihen, 1960b). Figs. 1, 2(8); Table 1. The pollen analysis by Kapp (1965) of the section vielding the Doby Springs fossils shows a distinct change in the floral composition between the lowest (locality 5 of Stephens, 1960) and the higher (localities 2 and 4) fossil-bearing horizons. The latter two localities, within a 60 cm unit, produced the turtles. The shrews come from locality 2, and the majority of the fish fauna was collected nearby from the unit immediately above (unit 21, locality 3 of Stephens, 1960). The following remarks apply to the fauna as represented by Stephens' localities 2, 3 and 4, all in the NE¼ of the SW section quarter. The majority of the molluscan species in the fauna are represented at locality 4 (Miller, 1966).

Species with presently northern distribution are Probythinella lacustris, Lymnea stagnalis jugularis, Vertigo elatior and Pupilla muscorum among the snails; the shrews Sorex arcticus, S. cinereus and large Blarina; the vole Microtus pennsylvanicus and the fish Perca flavescens. The hylid frog usually associated with cool, moist faunas, Pseudacris cf. P. triseriata, was present at one of the Doby Springs localities (Tihen, 1960b). Based on the species composition and the relative abundance of individuals representing taxa of presently northern distribution, Miller (1966) concluded that the Doby Springs assemblage represented the coolest climate in the sequence of five faunas he studied.

Correct stratigraphic placement of Doby Springs localities is difficult. The pollen composition of samples from locality 5 is similar to that from the Berends and Adams local biotas (Kapp, 1965, 1970); the three spectra are regarded by him as representative of an Illinoian maximum glacial interval. Due to the shift in composition encountered at localities 2 and 4, however, Kapp (1965) interprets them as occurring at a somewhat later time. Devore (1975) attaches stratigraphic significance to the four "northern" snail species mentioned above: they are not present in the Berends 1.b., abundant in the Doby Springs 1.b., and occur with increasing rarity in the Butler Spring and Sloth Locality assemblages, finally to disappear from the region by the time of the Mt. Scott l.b. This is also the rationale for Miller's (1966) arrangement, where the fauna indicative of the coolest climate is placed first, or oldest in the sequence.

Although the weight of evidence is in favor of retain-

ing the sequence proposed by Miller, I was struck by certain similarities between the mammalian segments of the Mt. Scott (see below) and Doby Springs biotas after determining that the unique aquatic emvdid, Chrvsemvs hibbardi, occurred in both and thus far is unknown from any other localities. Potentially significant mammals, shared by the Doby Springs and Mt. Scott assemblages and not known from other, presumably Illinoian, faunas in southwestern Kansas and northwestern Oklahoma, are Sorex arcticus, S. palustris. Zapus hudsonius transitionalis and Bison. The possible stratigraphic importance of this interesting similarity is negated in part, however, by morphological differences in the muskrats (Semken, 1966) and short-tailed shrews (Hibbard, 1963b) in the two biotas. Using Miller's (1966) listings, I also compared the overall molluscan compositions of the two faunas, which showed remarkable similarity. The correlation coefficient (defined as the number of species present in both faunas divided by the total number in the smaller, or less well-represented fauna, and expressed as a percentage) between Doby Springs locality 4 and Mt. Scott locality UM-K1-60 was 93%. At this point I would rather stress apparently similar climates and habitats in these two faunas rather than attach stratigraphic significance to correlations of species composition.

Further collecting at locality 2 would probably result in a more complete turtle complement, which most likely would amount to a typical transitional assemblage (see Summary below). Three of the recorded species, *Terrapene ornata, Chrysemys scripta* and *Chrysemys hibbardi*, are represented by single specimens each. Only *C. picta* was found in quantity.

Adams 1.b. SE¹/₄ Sec. 32, T 34 S, R 29 W, Meade Co., Kansas (E. H. Taylor, 1943; Tihen, 1955, 1962; Preston and McCoy, 1971. Faunal lists in Miller, 1966 and Schultz, 1969). Figs. 1, 2(9). Kapp (1965) was the first worker to treat (in publication) the fossils from the stratigraphically lower, basal, coarse sediments in the Butler Spring area as a separate biota. Previously, Hibbard and Taylor (1960) had included the vertebrates and molluscs from five localities in a single fauna. Kapp analyzed samples of fossil pollen from site 2 (Hibbard and Taylor, 1960) and found the spectrum to be similar to that of the Berends and locality 5 of the Doby Springs biotas. Samples from locality 1 of Hibbard and Taylor (1960) showed a possible decrease in the frequency of pine and marked increase in the proportion of juniper and hardwoods relative to the spectrum at locality 2. Since Kapp's publication the remaining localities (2, 3, 4 and 5) have been collectively designated the Adams 1.b.

As was mentioned above, a snail of presently southern distribution, *Helicodiscus singleyanus*, appears in this fauna and persists in the younger Butler Spring and Mt. Scott biotas. Molluscs of northern Recent distribution are also present, as is the vole *Microtus pennsylvanicus*. Although the turtle species present number only two, suggesting a depauperate fauna associated with a glacial maximum, the picture obtained from the species composition is not the same as in faunas from other intervals possibly associated with glacial maxima. The forms present are *Emydoidea* and *Chrysemys scripta*.

Sandahl 1.f. McPherson Co., Kansas (Semken, 1966; Miller, 1970; Holman, 1971; Lundberg, 1975). Herpetofaunal localities listed by Holman (1971). Figs. 1, 2(5). The sequence of local faunas in the Saline and Smokey Hill river valleys of central Kansas is currently under study by Zakrzewski and students (Zakrzewski, 1975). The correct sequence of these faunas has not been worked out, and correlation with the southwestern Kansas-Oklahoma Panhandle local faunas is difficult, in large part because zoogeographic and stratigraphic factors are both operating (Miller, 1970). The latitudinal separation is not great, but there is a 300 m difference in altitude and the east-west separation between the regions is some 250 km. Faunal comparisons based on the molluscan and mammalian segments show a moderately high degree of correlation between the Sandahl 1.f. and any of the localities in the Meade Co. area assigned to the Illinoian interval (tentative sequence: Berends-Mt. Scott local biotas). The two available specimens of Ondatra are in the size range characteristic of the Berends and Doby Springs biotas, although comparison of latitudes of areas of sympatry led Semken (1966) to conclude that the Sandahl l.f. may represent a slightly warmer climate.

The admixture of mammalian species of presently eastern and western distributions, and extinct large mammals normally associated with eastern (*Mylohyus*) or western (*Dinobastis*) forests led Semken (1966) to hypothesize the former existence of a gallery forest extending across the plains. Generally speaking the herpetofauna is composed of species occurring in the region of McPherson Co., Kansas, today, although the humeri of *Pseudacris triseriata* found in the Sandahl 1.f. have a character found in the subspecies maculata, presently occurring to the northwest of the fossil population (Holman, 1971). Two percid fishes in the fauna display southward or southeastern extensions of their Recent range boundaries. The chelonian segment of the fauna is most likely incomplete, consisting thus far of only two taxa: Trionyx sp. and Chrysemys scripta.

Williams 1.f. NE corner SE¼ Sec. 21, T 18 S, R 7 W, Rice Co., Kansas (Hall, 1972; McMullen, 1975; Lundberg, 1975). Figs. 1, 2(2). Molluscs from this fauna were listed by Hall. McMullen has studied the mammals and described a new species of shrew which is found also in the Duck Creek 1.f., 75 km to the northwest on the Smokey Hill River (McMullen, 1975). The latter fauna and the Angus 1.f. (see below) both contain the presently boreal vole, *Clethrionomys*. The turtles of the Williams 1.f., here listed for the first time, are all aquatic species: *Chelydra serpentina, Emydoidea blandingi, Chrysemys scripta* and *C. picta*. Permanent water and aquatic vegetation are implied. The remainder of the herpetofauna is currently under study.

Butler Spring l.b. NE¼ SE¼ Sec. 32, T 34 S, R 29 W, Meade Co., Kansas (G. E. Schultz, 1965, 1969; Miller, 1966; Brattstrom, 1967; Devore, 1975; Lundberg, 1975; Smith, 1958). Figs. 1, 2(9); Table 1. As mentioned above in the discussion of the Adams biota, this assemblage is restricted to the material collected from locality 1 of Hibbard and Taylor (1960). I have decided to follow Devore (1975), in treating this faunal horizon separately from the Sloth Locality, which had been considered part of the Butler Spring biota by Schultz (1969). The separation is supported by differences in the turtle segments of the faunas - particularly because of conspicuous, widely-spaced growth markings on plastral bones of Chrysemys picta collected from the Sloth Locality. Devore based her segregation of the two faunas on the apparent disappearance from the Sloth Locality of two molluscan species that presently occur, for the most part, in regions of cool climate. The preferred habitats of these snails are present in the Sloth Locality, so the conclusion reached is that it represents a warmer climate than the Butler Spring biota. Few mammals are available from the Butler Spring biota (restricted) for comparison with the Sloth Locality. Microtus pennsylvanicus occurs in both assemblages. The fish listings (Smith, 1958; Schultz, 1965) of the two faunas are similar.

The turtle remains present are of quality and quantity

to suggest fossilization at the depositional site. The species composition, especially the large member of the *Chrysemys floridana-concinna* complex, supports the concept of local habitat being that of a quiet portion of a large, permanent, slow-moving stream (Hibbard and Taylor, 1960; Schultz, 1965).

Sloth Locality (UM-K3-61) NW¼ NE¼ NW¼ Sec. 5, T 35 S, R 29 W, Meade Co., Kansas (Schultz, 1965; Devore, 1975). Figs. 1, 2(9); Table 1. The stratigraphic placement of this assemblage was discussed above (Butler Spring 1.b.). Mammalian species of presently northern distribution (Sorex cinereus, Spermophilus richardsoni, Microtus pennsylvanicus) are present.

The habitats depicted by previous authors (Schultz, 1965; Devore, 1975) are reflected in the composition of the cold-blooded vertebrate fauna. A large stream is indicated by the presence of fish genera *Lepisosteus* and *Ictalurus*. Occurrence of the green sunfish (*Lepomis cyanellus*) implies, in addition, a pond habitat, which is also preferred by *Kinosternon flavescens*. An upland, prairie situation nearby is required for some of the mammalian species present, as well as the ornate box turtle, found as associated fragments of a single individual. Mammalian and molluscan evidence of a marsh-border community is also afforded, and remains of *Emydoidea*, although consisting of only one rather worn peripheral bone, would be expected to result from this habitat.

Despite the probable stratigraphic differences between this fauna and the Butler Spring biota proposed by Devore (1975), the cold-blooded vertebrate segments collected at each locality could easily represent parts of a species composition unchanged in the time interval in question. The only possible zoogeographic (or stratigraphic) event would be the presence of *Chrysemys (Pseudemys) concinna* in the Butler Spring biota. Greater rainfall could be responsible for the low-gradient river habitat requirements of this species.

Thus far in this discussion we have seen a relative stability in the turtle fauna in the region of southwestern Kansas beginning at the time of the Berends l.b. Tortoises are apparently absent except in the Berends, and except for decreases in the number of species present in assemblages that are possibly associated with glacial advances, the composition of the aquatic portion of the vertebrate fauna is essentially constant. Considering this uniformity, and due to the lack of strict stratigraphic control, it will seem desirable to base conclusions about distributions during this interval on the preceding local faunas taken as a whole. Hibbard (1970) considered the preceding localities, with the exception of the Butler Spring l.b. and the Sloth Locality, as early Illinoian in age.

Better stratigraphic placement is possible for the remaining four pre-Wisconsinan biotas from Meade Co., in spite of the fact they occur over a 25 km stretch of territory (see Kapp, 1965, p. 175). A well-indurated massive caliche or its residuum is associated with the former High Plains surface in this area, and sections generally can be traced upward from fossil horizons to it. In the case of the Jinglebob l.b., the fossils are from a terrace deposit of a stream (possibly a meander of ancestral Crooked Creek) which participated in dissection of the surface at some time after the formation of the caliche. The Cragin Quarry fauna occurs in sediments about 3 m beneath the caliche; the silts in the Butler Spring area and the Mt. Scott fossil horizons lie at various distances below it (Schultz, 1969, Plate I).

I have relied heavily on Kapp's suggestions regarding the relationships between the post-Butler Spring localities on the XI Ranch and the Mt. Scott and Cragin Quarry localities on the Big Springs Ranch. For several reasons, including the unique character of the Cragin Quarry local fauna, containing mammalian and reptilian taxa peculiar to this assemblage, I have decided to deviate from Schultz's (1969) placement of the fauna from silts above the Butler Spring l.f. horizon on the XI Ranch as a Cragin Quarry equivalent. In the first place, an erosional unconformity may exist a short distance below the Cragin Quarry faunal horizon (Hibbard and Taylor, 1960, p. 29; Kapp, 1965, p. 231). In addition, Kapp (1965, pp. 207, 209) was impressed by the similarity in composition between the black silty clay overlying the fossil-bearing layer at the UM-K4-53 locality of the Mt. Scott biota and a zone rich in plant remains, possibly charred, below the fossil Gopherus burrow in the red sandy silts at locality UM-K3-59 on the XI Ranch. The proposed sequence which I have followed is summarized by Kapp (1965, p. 227).

The large Pleistocene box turtle belonging to the *Terrapene carolina* group makes its first known appearance in Kansas in the Mt. Scott biota. *Gopherus* reappears, possibly for the first time in this area since the Arkalon 1.f., in the XI Ranch localities. A large species of *Hesperotestudo* occurs with the *carolina*-group box turtle in the Cragin Quarry local fauna. Due to the fact that Meade Co., Kansas appears to be located



Figure 2. Late Pleistocene local faunas in Nebraska, Kansas, and the Oklahoma Panhandle, and approximate nearby Recent distributional limits of 4 species of aquatic emydid turtles. 1, Arkalon; 2, Williams; 3, Rezabek; 4, Berends and Nye Sink; 5, Sandahl; 6, Kanopolis; 7, Hay Springs and Rushville; 8, Doby Springs; 9, Adams, Butler Spring, Sloth Locality, Mt. Scott, Cragin Quarry, XI Ranch, Jinglebob, Jones; 10, Angus.

at the periphery of the late Pleistocene distributions of southern forms such as large carolina-group Terrapene, Gopherus and Oryzomys, the presence or absence of these forms serves only to distinguish faunas, and cannot be used to arrange them in temporal succession. Stratigraphy, together with faunal analysis, of the sequence Mt. Scott - Cragin Quarry - Jinglebob, clearly imply two mesic, equable intervals separated by a semiarid one. Relying on faunal evidence alone the stratigraphic ambiguities between the XI Ranch localities and the Mt. Scott sites, suggested by Kapp's (1965) proposed interpretation of the "organic" layers, would be resolved by placing the post-Butler Spring XI Ranch local fauna earlier than the Mt. Scott on the basis of its antedating the arrival of carolina-group Terrapene and Oryzomys. This would, of course, involve introducing the circularity I have been trying to avoid. Perhaps study of the molluscs from the XI Ranch localities, and of pollen potentially available from KU Loc. 7, as Kapp has suggested, will aid in providing independent evidence. In any case, the sequence seems to demonstrate considerable climatic fluctuation during the period in question.

Mt. Scott 1.b. Three localities, in Sec. 13 and 14, T 32 S, R 29 W and Sec. 18, T 32 S, R 28 W, Big Springs Ranch, Meade Co., Kansas (Hibbard, 1963b, 1970; Miller, 1966; Etheridge, 1961; Lundberg, 1975; Milstead, 1967; Preston and McCoy, 1971; G. R. Smith, 1963). Figs. 1, 2(9); Table 1. Hibbard (1963b), Kapp (1965) and Miller (1966) have all considered these localities as at least roughly contemporaneous. Fragments of Terrapene (carolina group) and Chrysemys picta occur at all three sites. The listing in Table 1 is restricted to UM-K1-60 (SW¼ SW¼ Sec. 13, T 32 S, R 29 W), and the following remarks apply to this locality. Six of the 14 species of fishes listed by Smith (1963) form an assemblage indicative of a gravel-bottomed, clear stream with moderate current and riffles. Additional fishes and part of the molluscan fauna represent a lacustrine or pond environment. A portion of the small mammal fauna would prefer a marshy environment, and nearby woodlands are indicated by some of the mammals and molluscs. The physical evidence summarized by Hibbard (1963b) suggests a stream 20 km or less in length fed by springs along its banks, and with impoundments in the valley probably due to the presence of beaver dams.

Shallow impoundments or sloughs would provide an ideal environment for the well-represented *Sternotherus*.

The marshy situation would be preferred by *Emydoidea*. *Carolina*-group *Terrapene* probably inhabited the adjacent woodlands. The habitat preference of *Chrysemys hibbardi*, found only in this locality and locality 2 of the Doby Springs biota, is, of course, unknown, but may have been restricted to larger ponds or lakes.

The interval beginning with the Mt. Scott biota and ending after the time of the Jinglebob biota is characterized by the appearance and subsequent disappearance in Meade Co. of two species with southern distributions, large *Terrapene* and *Oryzomys palustris*. In addition the least shrew, *Cryptotis parva*, and a small, presumably southern, race of *Blarina* are thought by Hibbard (1963b) to have moved into the area in Mt. Scott time. Miller (1966) includes 6 molluscan species of generally southern distribution in the Mt. Scott biota.

Ophisaurus attenuatus was recorded by Etheridge (1961), and further lizard and snake fossils are currently under study.

XI Ranch localities. Three of five localities listed by Schultz (1969) in Qpk₁ beds (Qs₁u of Hibbard and Taylor, 1960), Butler Spring area, XI Ranch, Meade Co., Kansas: (1) KU Loc. 7 (Dire Wolf locality), SW¼ SW¼ Sec. 33, T 34 S, R 29 W, Bed 4 of measured section (Hibbard and Taylor, 1960); (2) Locality UM-K3-59, NW¼ SW¼ Sec. 33, T 34 S, R 29 W, Unit 9 of measured section (Schultz, 1969); (3) UM-K2-62, NW¼ SW¼ Sec. 33, T 34 S, R 29 W (Kapp, 1965; Schultz, 1969; Tihen, 1960b). Figs. 1, 2(9); Table 1.

A nearly complete specimen of Gopherus was found in the remaining 60 cm length of a burrow at the base of the reddish sandy silt layer 120 m to the NE of UM-The field designations for turtle fragments K3-59. collected at the Gopherus locality, at UM-K3-59 proper and at UM-K2-62 are "Qs1u, reddish sandy silts" or "Gopherus horizon". Terrapene ornata occurs at the Gopherus locality and at UM-K2-62. Chrysemys scripta and Emydoidea are found at UM-K2-62 and Graptemys at the Gopherus locality. Except for the rarely-found Graptemys, the aquatic forms are duplicated at KU Loc. 7, which has also yielded Trionyx, Chelydra, and Chrysemys picta. Gopherus is also found at KU Loc. 7, but no Terrapene ornata material has been taken there. At the moment it seems reasonable to concur with Schultz (1969) in treating the fossils from these localities (including the Gopherus site) as a single fauna. From the older(?) Mt. Scott biota and the younger Cragin Quarry local fauna, the XI Ranch localities differ in containing Gopherus and Terrapene ornata. There is no sign of large carolina-group Terrapene, and I was unable to find any material referable to Hesperotestudo (=Geochelone, see Schultz, 1969) taken from the Gopherus horizon.

Cragin Quarry 1.f. SW¼ Sec. 18, T 32 S, R 28 W, Meade Co., Kansas. Locality 1 (Hibbard and Taylor, 1960), = KU Loc. 6, = USGS Cenozoic locality 21274. Figs. 1, 2(9); Table 1. (Hibbard and Taylor, 1960; Kapp, 1965; Auffenberg, 1966, 1974; Brattstrom, 1967; Etheridge, 1958, 1960b; Hay, 1917; Tihen, 1960a, 1960b). Previous authors (Etheridge, 1958, 1960b; Hibbard and Taylor, 1960) have concluded that the depositional site represents an oasis in an area experiencing semi-arid climatic conditions. At the locality itself were artesian springs with a local, possibly relict, population of spruce and pine. The available moisture in the environment was inadequate, however, to support much of an amphibious or aquatic-border community. Thus, according to Hibbard and Taylor (1960) the hygrophilic molluscan segment of the fauna is depauperate and the shrews and microtine rodents are represented only by the desert shrew and prairie vole, respectively. The majority of the small mammals, as well as the reptilian fauna, represent an upland assemblage tolerant of semi-arid conditions. A few large mammals requiring a moderate amount of browsing vegetation were, however, present in the area. According to the above authors only small fishes were represented at the depositional site.

The question of correlation with the XI Ranch localities cannot be resolved with absolute certainty on the basis of the cold-blooded vertebrate fauna, but to my mind the contrast between the Cragin Quarry fauna and the assemblage contained in KU Loc. 7, the Gopherus horizon at UM-K3-59 and UM-K2-62 is too great to be explained by differences in local habitat. None of the three turtle species found in the Cragin Quarry l.f. are known from the XI Ranch localities. The conspicuous terrestrial forms, Hesperotestudo and carolina-group Terrapene, could reasonably be expected in the XI Ranch localities if they were present in the area at the time. We are re-examining unreported lizard material from UM-K3-59 identified by Richard Etheridge. In a large number of specimens no Holbrookia texana or Phrynosoma modestum were noted. Schultz (1969) stressed the similarity in composition of the mammalian faunas represented in the Cragin

Quarry and XI Ranch sites. There are 8 species (including three carnivores) shared by the two assemblages and not present in the Mt. Scott l.b., but the 5 rodents are currently widespread plains inhabitants. On the other hand there are 6 species in the Cragin Quarry local fauna which are at present, or were presumed to have been, tolerant of arid conditions, or that are now living only in the southern Plains or Gulf coast. These forms have not been recorded from the XI Ranch localities.

Perhaps the most interesting observation made by Hibbard and Taylor (1960) concerned the segment of the molluscan fauna which is now generally northeastern in occurrence. Of this group of seven species only one is represented by a relict population in Meade Co. today. The authors suggest that artesian springs (still common in the area) provided suitable habitat for these forms in an otherwise semi-arid environment, and that their subsequent disappearance is due to the rigors of Wisconsinan alluviation and erosion.

Jinglebob 1.b. SW¹/₄ Sec. 32, T 33 S, R 29 W, Meade Co., Kansas (Hibbard, 1955, 1970; Brattstrom, 1967; Chantell, 1966; Etheridge, 1961; Lundberg, 1975; Milstead, 1967; Oelrich, 1953; Preston and McCoy, 1971; Tihen, 1954, 1960b). Figs. 1, 2(9); Table 1. This biota reflects an unusually humid, warm interval; a climate radically different from that of the present and not duplicated in any other known Pleistocene localities in Meade Co. A Gulfcoast element is evident among the mammals (Oryzomys) and possibly in the flora (see Kapp, 1965). Representatives of the Recent boreal fauna are few, particularly in the molluscan segment, and some snails of uncommon and potentially significant occurrence are present (D. W. Taylor, 1965). Perhaps the time of the Jinglebob biota corresponds with an extension of the southern forest soil to the north as documented by Ruhe (1974). The fossils provide the best-known of late Pleistocene snake faunas in Kansas, both in number of forms and available specimens. Brattstrom (1967) suggests a correlation between the increased number of large forms or individuals and warm climate, although it seems possible to attribute the phenomenon to good sampling. Species in the herpetofauna extralimital with respect to their Recent distributions include carolina-group Terrapene, Emydoidea, Ophisaurus attenuatus, and probably Pseudacris triseriata. The relatively small number of turtle and fish species in evidence may attest to the lack of a suitable

lacustrine habitat in the vicinity of the depositional site.

Radiocarbon-dated local faunas in southwestern Kansas and northeastern Oklahoma.- A sequence of these glacial-stage localities has recently been presented by Miller (1975), who, after study of the molluscs, was able to reach some general conclusions about the effects of climate during the Wisconsinan interval. For the most part local extinction occurred after the youngest of the faunas (ca. 10,500 yr.) and involved principally aquatic species and those of presently northern distribution. The proportion of climatically-tolerant species has, as a result, increased markedly in the Recent fauna. Hibbard (1970) listed mammals from some of these localities. Ranges of three shrews, Microtus, and to a lesser extent Zapus, have receded to the north or east in a fashion similar to that of molluscan forms since the time of the Robert 1.f. (ca. 11,000 yr.). It might be noteworthy that extinct large mammals found in the older Jones l.f. (ca. 28,000 yr.) are not present in the Robert horizon (Schultz, 1969).

Turning to the cold-blooded vertebrate segment represented in these faunas, we find a discouragingly small availability of identifiable fossil remains. I have found only a few fragments of turtle bones in a perusal of Jones, Bar M, and Robert local faunas. Those that are identifiable can be referred to *Chrysemys picta*, and thus far there is no indication that any other species are represented. To date, two taxa of snakes (Brattstrom, 1967) and a catfish (Lundberg, 1975) have been reported from the Jones 1.f. (see Hibbard, 1970, for bibliography). It is hoped that further collection and study by Carson Davis will add to the small amphibian fauna known from the Jones locality (Tihen, 1942, 1955, 1960b, 1962; Chantell, 1966).

It is premature to speculate on what the overall composition of the cold-blooded vertebrate fauna was like during this interval. Given the reasonably extensive amount of collecting from radiocarbondated faunas in the region of southwestern Kansas, I think it is safe, however, to conclude that the lizard (see Etheridge, 1961) and turtle components were markedly reduced in comparison to early- or pre-Wisconsinan assemblages in the area and, in addition, relative to the Recent fauna.

Nebraska

Thanks to the courtesy of Michael Voorhies and others at the UNSM, Larry Martin and Donald Baird, I had the opportunity to study the turtles from two areas in Nebraska from sediments younger than the Type "O" ash fall of ca. 0.6 x 10⁶ yr. Stratigraphy and mammalian paleontology suggest similar ages for these faunas, and they serve as representation of the northern aspect of the Plains assemblage prior to Wisconsinan glaciation.

Rushville 1.f. NE¼ NW¼ Sec. 9, T 29 N, R 44 W, Sheridan Co., Nebraska. UNSM Localities Sh-3 and Sh-4, 460 m ENE of Sh-3 (Schultz and Tanner, 1957; Schultz and Martin, 1970; Schultz, et al., 1972). Figs. 1, 2(7); Table 1. Using Semken's (1966) chronocline for muskrats (Ondatra), C. B. Schultz, et al. (1972) have placed the Hay Springs (upper level), Rushville and Gordon 1.f.'s in Sheridan Co. in the same time interval. Semken had found the Hay Springs Ondatra nebrascencis similar in size to representatives from the Doby Springs and Berends assemblages in northwestern Oklahoma. The generic composition of the Rushville rodent segment is otherwise similar to these latter faunas.

The turtles are represented by numerous specimens, and I believe they constitute a complete fauna. Since the time of the earlier, Blancan, Sand Draw (Holman, 1972a) and Lisco (Preston, in preparation B) local faunas, the northern limits of Kinosternon flavescens and Chrysemys scripta had probably receded to the south in the High Plains, and Hesperotestudo had become locally extinct. Late Pleistocene environments were suitable for Terrapene ornata and Emydoidea; Chelvdra, Chrvsemvs picta and Trionyx spinifer persisted. The Recent fauna of Sheridan Co. is reduced to Chelydra, Chrysemys picta and Terrapene ornata. The western limit of Emydoidea is now 160 km to the east, and no records of Trionyx spinifer exist from the Niobrarra drainage although relict populations are known further north and west - in the headwaters of Chevenne drainage in Wyoming and in the Yellowstone and its tributaries in Montana (Webb, 1962).

Terrapene ornata would have preferred open country in the uplands, and the presence of *Emydoidea* suggests the availability of marshy or pond habitats in the area.

Angus I.f. SW⁴ NE⁴ Sec. 33, T 4 N, R 6 W, Nuckolls Co., Nebraska. UNSM Loc. No-101 (Schultz and Tanner, 1957; Martin, 1969; Schultz and Martin, 1970). Figs.

1, 2(10); Table 1. This fauna is found in association with a buried soil complex which lies stratigraphically below the Loveland loess. It bears, therefore, the same qualitative relationship to the overlying Loveland, containing a pre-Wisconsinan (?Sangamonian) paleosol as does the Rushville horizon. Schultz and Martin pointed out a similarity between the Angus fauna and the Cragin Quarry and Jinglebob local faunas of Meade Co., Kansas. Many of the mammals (Taxidea, Reithrodontomys, Synaptomys, etc.) and, in particular, the tortoise (Hesperotestudo), would indicate a relationship to the Mt. Scott-Cragin Ouarry section and the post-Butler Spring XI Ranch localities. The stratigraphic data, however, and the assignment of the muskrat to the form Ondatra nebrascensis, would favor at least approximate correlation with the earlier Berends and Doby Springs l.f.'s.

The turtle segment of the fauna (Table 1) is probably incomplete (where are *Terrapene ornata, Graptemys,* and *Trionyx*, for example?); however, *Chrysemys scripta* is present, possibly slightly extralimital to its present distribution to the southeast. Most important, a representative of the large lineage of *Hesperotestudo* was taken. This location is, to date, the northernmost record for this extinct genus in the late Pleistocene of North America.

In the remarks following the systematic presentation of *Chrysemys picta* I have commented on possible climatic indications afforded by growth marks on the *picta* specimens together with the large size attained by *Chrysemys scripta*.

Oklahoma, Texas and New Mexico

The majority of late Pleistocene records of turtles and alligators from this region have been previously published. I have added *Kinosternon flavescens* from the Berclair 1.f., Bee Co., Texas; *Terrapene carolina* from Navarro and Hardin Co.'s; a duplicate record of *T. ornata* from the Brown Sand Wedge 1.f.; *Graptemys pseudogeographica* from the Pitt Bridge and Batte gravel pit localities; *Chrysemys scripta* from the Berclair 1.f. and Batte gravel pit; *Chrysemys ?concinna* from the Berclair 1.f. and *Gopherus* from a gravel pit in Haskell Co., Texas. The *Kinosternon* and *Gopherus* were identified by Ernest Lundelius. *Graptemys geographica* from the Trinidad 1.f., Henderson Co., Texas, was re-identified as *Chrysemys scripta*, and the record of this species from the Moore Pit 1.f. is questioned (see Systematic List of Species).

I have omitted exact locality information from the following brief discussions of a selected series of faunas based mainly on the summaries of Lundelius (1967) and Slaughter (1967). Treatment of the Ingleside fauna (see Fig. 3) and local faunas (e.g., Ben Franklin, Cave Without a Name) from which good representations of snakes, lizards and amphibians are available will be postponed. In addition to the literature reviewed by Holman (1969b) I have drawn upon reports of Semken (1961), Dalquest (1964), Lundelius (1963, 1972), Johnson (1974) and Gillette (1974). I have also considered further material described by Hay (1911, 1916, 1923, 1924 and 1927).

Slaton 1.f., Lubbock Co., Texas (Dalquest, 1967; Holman, 1969a,b; Milstead, 1967). Figs. 1, 3. This is undoubtedly the oldest of the late Pleistocene faunas from the southern section of the Plains that are con-Some controversy exists, sidered in this discussion. however, as to its placement. A later (Sangamonian) age was favored by Taylor (1965), which would then imply that the arrival of carolina-group Terrapene in the Plains was more-or-less simultaneous and widespread, including the Slaton location and the Mt. Scott-Cragin Quarry section in Kansas, some 430 km to the north. But Dalquest (1967) thought the fauna probably antedates the arrival of Bison, and Hibbard (Hibbard and Dalquest, 1973) was of the opinion the occurrence of Neofiber implied the close contemporaneity of the Slaton, Rezabek and Kanopolis faunas. T. carolina is not known from the latter two assemblages. Whatever the case the appearance of carolina-group Terrapene in the Slaton l.f. probably stands as the earliest documentation of the arrival of the large box turtles in the Plains that is known to date. Except for this form and Alligator, the herpetofaunal elements are all found in Lubbock Co., Texas, today.

Easley Ranch 1.f., Foard Co., Texas (Dalquest, 1962; Holman, 1962; Lynch, 1964; Gehlbach, 1965; Lundberg, 1967, 1975). Figs. 1, 3. This represents the earliest in a sequence of faunas discussed by Slaughter (1967), beginning with the Easley Ranch (>50,000 yr.) and ending with the last assemblages (Brown Sand Wedge, Domebo) that predate the interval (8-10,000 yr.) of



Figure 3. Late Pleistocene fossil localities and records of turtle and alligator species in Texas, New Mexico and Oklahoma. References for turtles and Alligator only are cited for localities not discussed in the text. Circle, Ingleside 1.f., San Patricio Co., Texas (Auffenberg, 1962a; Bramble, 1971; Gillette, 1974; Hay, 1926; Holman, 1969b; Lundelius, 1972; Slaughter et al., 1962): Alligator, Trionyx spinifer, Terrapene carolina, Chrysemys scripta, Gopherus sp., Hesperotestudo sp. (listed in Lundelius, 1972). Square, Lubbock Lake site (see text). Star, Clear Creek 1.f. (see text). Triangle, Pitt Bridge localities (see text). Diamond, Berclair 1.f. (see text). Tri

major extinction. The sequence demonstrates a stretch of time characterized by disappearance of presumably heat-intolerant species and the arrival of Sigmodon (Easley Ranch to Moore Pit), followed by a period of dessication as suggested by the presence of forms, now occurring to the west and southwest (Cynomys, Onychomys, Notiosorex), represented in the Clear Creek and Sims Bayou 1.f.'s. At some time after 21,000 yr. (Bar M 1.f.) and by the time of the Howard Ranch assemblage (ca. 18,000 yr.), molluscan and mammalian taxa now occurring to the north of northern Texas had re-occupied the area, and the northern limit of the armadillo, Dasypus bellus, was displaced southward. Slaughter (1967) considered this to be the period when giant tortoises disappeared. This question will be considered in more detail below. The "northern" forms persisted until the interval of major extinction, prior to which time supposedly cold-intolerant species such as Dasypus, the giant armadillo Holmesina, and Sigmodon were sympatric with the "northern" species. The dwarf Hesperotestudo is also present until around 11,000 yr. Some mammals surviving extinction underwent considerable range contraction or shifting to the northwest or northeast in Texas between the end of this interval and the present. Patterns of distributional change in the reptiles and amphibians are in many cases similar, as will be seen in the remainder of this discussion.

The Easley Ranch fauna contains one of only five published records of *Gopherus* from the late Pleistocene of Texas. Fragmentary remains of *Hesperotestudo* were also recovered. Foard Co., Texas, lies at the western edge of the principal ranges of *Thamnophis sirtalis, Storeria dekayi* and *Opheodrys aestivus* at this latitude. In addition to these species *Ambystoma*, *Hyla, Pseudacris*, and *Acris* are represented in the fauna as well as *Syrrhophus marnocki*, which occurred in the earlier Vera faunule (?Cudahy fauna) of adjacent Knox County, and which presently is found only north to 31° latitude, 300 km to the south of Foard Co.

Moore Pit 1.f., Dallas Co., Texas (Slaughter, 1966a; Gillette, 1974; Holman, 1969b; Lundberg, 1975; Milstead, 1967; Uyeno and Miller, 1962). Figs. 1, 3; Table 1. Slaughter *et al.* (1962) have discussed the stratigraphy of the second Trinity River terrace (Hill Gravels member, Lower and Upper Schuler members). The various localities of the Moore Pit 1.f. are listed by Slaughter (1966a). The complete shell of a large *Hesperotestudo* figured by Hibbard (1960) came from the Hill Gravels member. According to Slaughter *et al.* (1962) a slight unconformity occurs between the Hill

Trionyx sp.: Moore Pit 1.f., Dallas Co. (see text); Sims Bayou 1.f., Harris Co. (see text); Damp and Centipede Caves, Val Verde Co. (Lundelius, 1963); Quitaque l.f., Motley Co. (Dalquest, 1964). CS, Chelydra serpentina: Howard Ranch l.f., Hardeman Co. (see text). TC, carolina-group Terrapene: Curry and Roosevelt Co.'s, New Mexico (see text); Domebo site, Caddo Co., Oklahoma (see text); Logan Co., Oklahoma (Milstead, 1967). The following localities in Texas are discussed in the text: Slaton l.f., Lubbock Co.; Lewisville site, Denton Co.; Sims Bayou I.f., Harris Co.; Howard Ranch I.f., Hardeman Co.; Friesenhahn Cave, Bexar Co. The following localities are discussed in Milstead, 1967, and Holman, 1969b: Archer Co.; Dallas Pits, Dallas Co.; Henderson Co. (see also Gillette, 1974); Pitt Bridge, Brazos Co.; Duval Co.; Bee Co.; Atascosa Co.; Kincaid site, Uvalde Co.; 3 localities in Travis Co.; Cave without a Name, Kendall Co.. Additional records: Longhorn Cavern (Semken, 1961; Milstead, 1967); Sour Lake deposits, Hardin Co., part of holotype of Trachemys trulla (Hay, 1908, 1924; see Systematic List, in text); Batte gravel pit, Milam Co. (see text); Burnet Cave, Eddy Co., New Mexico (see text); Trinity River terrace, Navarro Co. TO, Terrapene ornata: Curry Co., New Mexico (Milstead, 1967); Roosevelt Co., N.M. (see text, Brown Sand Wedge 1.f.). Gsp, Graptemys sp.: Moore Pit 1.f. (see text); Pitt Bridge (see text); Batte gravel pit, Milam Co. (see text). TrS, Chrysemys (Trachemys) scripta: Hardin Co., part of holotype of Trachemys trulla Hay (see text); Sims Bayou l.f., Harris Co. (see text); Trinidad l.f., Henderson Co. (Stovall and McAnulty, 1950; see text); Batte gravel pit, Milam Co. (see text). Trsp, Chrysemys, subgenus Trachemys or Pseudemys: Howard Ranch 1.f., Hardeman Co. (see text). Quitaque l.f., Motley Co. (Dalquest, 1964). Goph, Gopherus sp.: Wheeler Co. (Auffenberg, 1962a; Bramble, 1971; Holman, 1969b); Haskell Co. (see text); Easley Ranch l.f., Foard Co. (see text); Atascosa Co., holotype of G. atascosae Hay (see text). Hsp, large Hesperotestudo: Easley Ranch l.f., Foard Co.; Moore Pit l.f. and Trinity River terrace at Carrollton (Hay, 1916), Dallas Co.; Longhorn Cavern, Burnet Co. (Semken, 1961); Sour Lake, Hardin Co. (Hay, 1924); Sims Bayou l.f., Harris Co.; Brazos terrace near Waco, McLennan Co. (Hay, 1916). ?Hsp, tortoise, Quitaque 1.f., Hall Co. (Dalquest, 1964). HW, Hesperotestudo wilsoni: Friesenhahn Cave, Bexar Co.; Brown Sand Wedge I.f., Roosevelt Co., N.M.; Domebo site, Caddo Co., Oklahoma (see text). A, Alligator cf. mississippiensis: Slaton 1.f., Lubbock Co.; Moore Pit 1.f., Dallas Co.; Sims Bayou 1.f., Harris Co. (see text). Iron Bridge 1.f., Rains Co. (Slaughter et al., 1962; Lundelius, 1972). McLennan Co. (Hay, 1924; Holman, 1969b). Portions of distributional boundaries for recent Terrapene carolina and Graptemys geographica are according to Conant, 1975.

Gravels and Lower Schuler. Slaughter (1966a) has listed *Terrapene carolina*, which was examined by Milstead (1967), and *Graptemys geographica* from the Lower Schuler. The occurrence of this latter species in the Trinity River terrace of Dallas and Henderson Counties is considerably extralimital to its present distribution (see Fig. 3). Additional *Terrapene* material from the Coppell site in Dallas Co., now correlated with the Moore Pit 1.f., has been identified as *T. carolina triunguis* by Gillette (1974). *Alligator* (in both Hill Gravels and Lower Schuler), *Coluber constrictor* and a frog are represented in Moore Pit sites along with the three turtles.

Lewisville Site, Denton Co., Texas (Slaughter et al., 1962; Slaughter, 1967; Milstead, 1967; Holman, 1966a, 1969b). As of Slaughter et al. (1962), fossils were all from the Upper Schuler member of the second Trinity River terrace. Large Hesperotestudo and carolina-group Terrapene are both present, as in the Moore Pit 1.f.

Pitt Bridge localities, Brazos and Burleson Co.'s, Texas (Hay, 1916, 1923, 1924; Gehlbach, 1965; Milstead, 1967; Holman, 1969b; Lundelius, 1972; Auffenberg, 1974). These localities are noted as "probably Aftonian" in the Hay citations and in Auffenberg (1974). They are designated early Pleistocene in Holman (1969) and Illinoian in Gehlbach (1965). Lundelius (1972) suggests a younger, perhaps Sangamonian, age in comparing these localities to the Ingleside l.f. For the present I will regard the various localities (Hay, 1924, p. 245) to be contemporaneous. At least one of them yielded Bison. The turtle species recovered are Trionyx spinifer, Terrapene carolina (see Milstead, 1967), Graptemys pseudogeographica and large Hesperotestudo. The Graptemys was reported by Hay (1923, 1924) as Chrysemys belli.

Berclair 1.f., Bee Co., Texas (Hay, 1924; Slaughter et al., 1962; Milstead, 1967; Holman, 1969b; Lundelius, 1972). The localities constituting this fauna are considered by Slaughter et al. (1962) and Lundelius (1972) to be late Pleistocene in age. Bison is present. The turtles are Kinosternon flavescens, Terrapene carolina, Chrysemys scripta and, possibly, Chrysemys concinna. The Kinosternon locality is given as Blanco Creek, Buckner Ranch site 1.

Batte gravel pit, Milam Co., Texas (Hay, 1927, p.

294). This locality, given as 3 mi. east of Cameron, is considered late Pleistocene based on the occurrence of *Terrapene carolina*. *Graptemys pseudogeographica* and *Chrysemys scripta* are also present.

Clear Creek 1.f., Denton Co., Texas (Holman, 1963, 1969b; Gehlbach, 1965; Uyeno, 1963; Lundberg, 1975; for further references see Hibbard, 1970). Figs. 1, 3; Table 1. This is the earliest fauna in this late Pleistocene sequence for which a finite radiocarbon date is available (ca. 28,000 yr.). It is from deposits in the same terrace fill as the Moore Pit and Lewisville localities and stratigraphically above their horizons. The six turtle species are listed in Table 1, along with Graptemys from the Moore Pit.

Denton Co., Texas, is situated in an interesting location zoogeographically, about half-way between the borders of the Austroriparian (to the east) and Kansan (to the west) biotic provinces of Blair (1950). Some taxa, such as Arizona, Cynomys and Onychomys, which occur in the Clear Creek 1.f. have their present eastern limits somewhat to the west of the faunal site. The western edge of Ophisaurus, Virginia, Opheodrys aestivus and Agkistrodon piscivorus lie in similar locations, and their expected presence is noted in the fauna. Likewise, Cnemidophorus gularis and Heterodon nasicus, whose eastern range limits lie to the east of the Clear Creek site, are also represented. Forms (e.g., Macroclemys, Sternotherus carinatus) whose western limits lie to the east of Denton Co., more or less at the border of Blair's Texan and Austroriparian biotic provinces, apparently do not occur in the Clear Creek l.f., however.

In addition to these geographic relationships, it should be noted that Denton Co. lies a short distance to the west of the border between the Gulf Coastal Plain and the Central Lowland physiographic province of Fenneman (1931). The western or eastern limits of numerous reptiles and amphibians coincide with this boundary, at least at the latitude of Denton Co. Of these, some (Ambystoma texanum, Rana utricularia, Sternotherus odoratus, Terrapene carolina) occur in the Clear Creek 1.f., and some (Kinosternon flavescens, K. subrubrum, Chrysemys floridana hoyi and Deirochelys, as well as several amphibians and squamate reptiles) are not known from the fauna. Generally speaking, the forms present suggest no great differences between distributional patterns at the time of the Clear Creek l.f. and those of the present, except for the eastward extensions noted above.

Sims Bayou 1.f., Harris Co., Texas (Slaughter and McClure, 1965; Holman, 1965, 1969b; McClure and Milstead, 1967). Figs. 1, 3. Assuming that the earliest appearance of Sigmodon in the southwest is recorded in the Moore Pit 1.f., Slaughter places the time of the Sims Bayou 1.f. as post-Moore Pit. Cynomys, Onychomys and Neotoma micropus are present, as well as Sigmodon, indicating a climate similar to that of the Clear Creek 1.f. Large Hesperotestudo is present, along with Alligator, Chrysemys (Trachemys) scripta, Trionyx, and carolina-group Terrapene (referred to T. carolina triunguis by McClure and Milstead, 1967). One of only 2 fossil records of Amphiuma is from the Sims Bayou locality (see Holman, 1969b).

Howard Ranch 1.f., Hardeman Co., Texas (Dalquest, 1965; Holman, 1964, 1969b; Gehlbach, 1965; Lynch, 1966; Milstead, 1967). Figs. 1, 3. This assemblage is called Groesbeck Creek in Holman (1964) and Slaughter (1967). Actually two sites, with radiocarbon dates ca. 17,000 yr. and 19,000 yr., produced this fauna which was taken from a basin fill (Groesbeck Creek fm.) consisting of stream and marsh deposits. The fauna may represent the conditions of the Wisconsinan glacial maximum, with a return of presently northern mammalian and molluscan species such as were last seen in the Easley Ranch 1.f. Climatic equability is demonstrated by the presence of Sigmodon and Orvzomvs and by Arizona and Agkistrodon in the snake fauna, along with the northern forms. Tortoises have not been found in the fauna. The only documented Texas Pleistocene occurrence of Chelydra is in this fauna, although no particular meaning is to be attached to this fact. It is not altogether surprising that snapping turtles are rare or absent in cave and river-terrace deposits. Chrysemys (?Trachemys) and a large Terrapene are also found in the Howard Ranch assemblage. Ambystoma texanum occurred here, slightly beyond its present distributional limit to the east of Hardeman Co.

Friesenhahn Cave, Bexar Co., Texas (Auffenberg, 1958, 1962b, 1974; Bramble, 1971; Gehlbach, 1965; Hay, 1916, 1924; Holman, 1969b; Mecham, 1959; Milstead, 1956, 1967; Tihen, 1962. For recent bibliography see Hibbard, 1970). Figs. 1, 3. Apparently the deposits in the Friesenhahn Cave represent an admixture of ages: according to Milstead (1967), 14,000-10,000 yr. B.P.; according to Hibbard (1970), middle to late Wisconsinan. Recent excavations have produced

the typical Friesenhahn assemblage (including *Hesperotestudo wilsoni*) with associated radiocarbon dates ranging from 17,000-19,000 yr. (R. W. Graham, personal communication).

The carolina-group box turtles of Friesenhahn Cave were assigned to the recent subspecies *triunguis* by Milstead (1967). Their average size was somewhat larger than a Recent population of *triunguis* from central Texas, and some of them displayed characteristics of shape similar to the older, giant form known as T. carolina putnami.

I shall postpone a discussion of differences in faunal composition between the late Wisconsinan assemblages of the Edwards Plateau region and the Recent fauna until the amphibians and squamate reptiles are reviewed. Meanwhile the summaries of Lundelius (1967) and Holman (1969b) should be consulted.

Brown Sand Wedge 1.f., Roosevelt Co., New Mexico (Gehlbach, 1965; Milstead, 1967; Slaughter, 1975). Figs. 1, 3. The box turtles *T. carolina* and *T. ornata* reported by Milstead (1967) from localities in the Blackwater Draw in the vicinity of Clovis, N.M., are also represented in the Sam Sanders gravel pit, 3 mi. north of Portales. Excavations at this site produced the Brown Sand Wedge 1.f. and yielded also a specimen of *Hesperotestudo wilsoni*. The radiocarbon date of this fauna is *ca.* 11,000 yr.

Domebo locality, Caddo Co., Oklahoma (Auffenberg, 1964; Slaughter, 1966b; Milstead, 1967). Figs. 1, 3. At this site the extinct *Hesperotestudo wilsoni*, and carolina-group box turtles extralimital to the present distribution of *T.c. triunguis*, are found with early man of the Plano Culture (Haynes, 1970) approximately 11,000 yr. ago.

Lubbock Lake site, Lubbock Co., Texas (Johnson, 1974). Figs. 1, 3. Three Paleo-Indian horizons at this locality demonstrate the probable disappearance of carolina-group Terrapene between 11,000 (Clovis horizon) and ca. 10,000 yr. (Folsom horizon). Kinosternon flavescens appears in the Folsom horizon. Terrapene ornata and Chrysemys scripta occur in all three horizons. Trionyx and Ictalurus were recovered only from the Clovis horizon. Additional reptiles and amphibians are currently being studied by T. R. Van Devender.

Illinois, Missouri, Arkansas and Mississippi

Milstead (1967) examined late Pleistocene carolinagroup Terrapene from Coles Co., Illinois, Franklin and Moniteau Co.'s, Missouri, and Marion Co., Arkansas. Mehl (1962) mentions an additional specimen of large Terrapene from Perry Co., Missouri. Terrapene from the Crankshaft Cave, Jefferson Co., is tentatively identified as T. ornata on the basis of small size (Parmalee, et al., 1969). The Jones Spring in Hickory Co. (Van Devender and King, 1975; Moodie and Van Devender, 1977), dated >40,000 yr., yielded a large carolina-group box turtle and Chrysemys scripta. The Brynjulfson Cave No. 1 in Boone Co. also produced Terrapene and, in addition, Chelydra and Emydoidea, which was known previously from the Enon Sink l.f., Moniteau Co. (see Preston and McCoy, 1971). In early or middle Wisconsinan time Emydoidea ranged as far south as 33°30' north latitude in Mississippi at the Catalpa Creek site (Jackson and Kaye, 1974, 1975; Holman, 1976), where it occurred with large Hesperotestudo.

Trionyx spinifer, Chelydra serpentina and Chrysemys scripta are known from the Wisconsinan of Sangamon Co., Illinois (Holman, 1966b). Galbreath (1938) recorded Chrysemys ?scripta and ?C. picta from the Polecat Creek 1.b., Coles Co., Illinois.

Mehl (1962) notes the occurrence of *Alligator* in two late Pleistocene localities in Missouri. One is from the Herculaneum 1.f., Jefferson Co. (Olson, 1940), from which unidentified turtle fragments were collected.

Selected records from the Eastern and Western United States

Holman (1967) reported the surprising occurrence of *Clemmys insculpta* from the Ladds Site, Bartow Co., northwestern Georgia. Holman (1976) has discussed the importance to concepts of late-Pleistocene climatic equability of various sympatric occurrence of reptiles and amphibians in the southeastern U.S. Wilson and Zug (1966) reported a specimen of *Graptemys pseudo-geographica* from the Wisconsinan of the Saginaw Bay in Michigan, extralimital to the present distribution of this species. *Terrapene carolina* appears, along with *Neofiber* as in the Slaton 1.f., in the Port Kennedy Cave, Montgomery Co., Maryland (see Milstead, 1969, p. 35).

Moodie and Van Devender (1978) noted the late Pleistocene occurrence of *Terrapene ornata* in Cochise Co., Arizona, near the western extent of the Recent distribution of this species. A Blancan specimen of *T. ornata* was also reported from the same area. Van Devender and Tessman (1975) recorded *Chelydra serpentina* from west of the continental divide in southern Nevada in late Pleistocene time.

Summary .- Only three late Cenozoic faunal intervals producing turtles are known from northern or western Nebraska: late Blancan (Sand Draw and Lisco 1.f.'s), late Pleistocene (Rushville 1.f.) and the Recent fauna (known from the last 100 yr. or so). Chrysemys picta is known in all three intervals and Trionyx spinifer, apparently, remained until the late Pleistocene but disappeared from this area by modern times. The northern limits of Kinosternon flavescens and Chrysemys scripta had moved to the south by the time of the Rushville 1.f., and local extinction of two tortoises (genus Hesperotestudo) seems to have had occurred before the Rushville - Hay Springs - Gordon interval. Three of the four remaining turtle species (in addition to C. picta) in the Recent fauna of north-central Nebraska were also present in the Rushville horizon but are unknown from the late Blancan faunas: Chelydra serpentina, Terrapene ornata and Emydoidea blandingi, although the nearest Recent record of this latter species is now some distance to the east of Sheridan Co. I believe the five species listed for the Rushville l.f. constitute the complete turtle fauna for the area at that time. In southern Nebraska, presumably during the same interval (Angus 1.f.), Chrysemys scripta still occurred, possibly somewhat north of its present northern limit, and the genus Hesperotestudo makes its northernmost known appearance in the late Pleistocene.

In the area of southwestern Kansas the Blancan turtle fauna as a whole lost only one member, *Macroclemys temmincki*, on a permanent basis when compared to the later Pleistocene faunas taken together. Tortoises, however, occur only sporadically in the late Pleistocene localities. The smaller form, a member of Auffenberg's (1963) *turgida* line, disappeared after the time of Berends 1.f. Large *Hesperotestudo* is only seen in the Cragin Quarry 1.f. *Gopherus* is thus far known only in the Arkalon 1.f. and post-Butler Spring, pre-Cragin Quarry XI Ranch localities.

Members of the Recent turtle fauna of Meade Co., Kansas, were all present in the late Pleistocene localities collectively, and were also found in Blancan faunas in

western Kansas. Nothing new has been added. During the late Pleistocene, however, the aquatic genera (or subgenera) Sternotherus, Graptemys and Chrysemys (Pseudemys, floridana-concinna section) appeared frequently in central and southwestern Kansas. These occurrences are all in climatically equable faunas, with admixtures of currently northern and southern taxa. and with evidence of greater available moisture than exists in these areas presently. Emydoidea blandingi was a common inhabitant of the region after its reappearance (apparently for the first time since the late Pliocene) in the Arkalon 1.f., and until the early Wisconsinan glacial interval. During or after the Wisconsinan Emydoidea's range shifted or contracted drastically to the northeast. The terrestrial emvdid, Terrapene carolina, appeared (or reappeared) in the Plains during the late Pleistocene. Its sojourn in Meade Co., Kansas, lasted, at least intermittently, from the time of the Mt. Scott l.f. to that of the Jinglebob l.f., concurrently with the spread of the rice rat, Oryzomys, to this area.

An attempt to characterize local faunas in southwestern Kansas as glacial, interglacial or transitional on the basis of the turtle species complement appears to succeed, at least to some extent, if it is assumed that the habitats represented and collecting efforts expended were sufficient to provide a more-or-less representative set of fossil specimens. If "glacial" faunas are taken to be those containing predominantly or exclusively presently northern species, then the turtle complement turns out to consist only of Chrysemys picta (radiocarbon-dated Wisconsinan Meade Co. localities discussed previously). Evidence of pronounced alluviation (basal gravels in a formation) might be another sign of a glacial maximum, but in the case of the Adams l.f. a different complement is noted (Emydoidea and Chrysemys scripta). "Interglacial" faunas are characterized by the presence of cold-intolerant species or those known to be adapted to xeric environments, with a concomitant decrease in the frequency of presently northern forms. In these faunas many aquatic species are rare or absent (notably Chrysemys picta in the Kanopolis and Cragin Quarry local faunas). Tortoises become conspicuous. Large carolinagroup Terrapene are common in the Slaton (in Texas) and Cragin Quarry faunas. This indicates either an interglacial climate (as represented by these faunas) less severe than that of the present, with a betterforested savannah habitat, or a habitat requirement for the large box turtles of this period considerably

different from that associated with modern T. carolina triunguis or T. c. major. The remainder of the faunas, with their large representation of turtle species of diverse habitat preferences, could be termed "transitional". Many of these assemblages, the Doby Springs and Mt. Scott, for example, not only display species compositions resulting from equable climates, but contain evidence of displacement of presently boreal forms to the south. The latter phenomenon has led some workers to identify these faunal compositions as representing stades within an interval of fluctuating glaciation. Compared to the relatively depauperate compositions represented by the faunas associated with glacial "maxima" (Cudahy and middle-late Wisconsinan assemblages in Meade Co.), these climatically equable faunas might better be termed "parastadial", with the prefix "para-" applying either temporally or spatially (next to, or near, in time or geographic location) to a glacial This minor nomenclatural suggestion is maximum. motivated by the analyses of late Pleistocene faunas by Semken (in preparation) and Zakrzewski (personal communication).

A more generalized analysis of compositions of late Pleistocene turtle faunas, depending less on presumed glacial or interglacial intervals or completeness of representation, is presented in Table 2. It should be noted that Chrysemys picta and Emydoidea blandingi are known from essentially all pre-14C-dated local faunas except for the Kanopolis, in central Kansas, and the Cragin Quarry (restricted). In the category of permanent residents, I have assumed that Kinosternon flavescens is frequently absent due to unsuitable habitat at the depositional site, although there is some evidence of distributional instability for this species. The same explanation, or the possibility that remains might be dispersed and obliterated by stream action, applies to the frequent rarity or absence of Chelydra and Trionyx. Some possible invaders from the Gulf Coast and Mississippi drainage, such as Sternotherus carinatus, Kinosternon subrubrum, Trionyx muticus, Macroclemys and Deirochelys, have not been seen in the Pleistocene of this area or further south in northeastern Texas. When the central Kansas faunas are better known, it may turn out that the generalized analysis summarized in Table 2 may apply to them also. Five expected "permanent residents" (Chelydra serpentina, Trionyx sp., Emydoidea blandingi, Chrysemys picta and C. scripta) are now known from the Sandahl and Williams local faunas taken together. Sternotherus, Graptemys and Chrysemys concinna may

 TABLE 2.
 Proposed effects of climate and habitat on movements of turtle species in southwestern Kansas and northwestern

 Oklahoma during the late Pleistocene.

More-or-less permanent residents ¹	From east or southeast. Effective precipitation, low-gradient streams	From south. Mild winters ²	Unknown
Kinosternon flavescens*	Sternotherus odoratus		
Trionyx spinife	r*		
Chelydra serper tina*	1-		
Terrapene ornata*		Terrapene carolina	
Emydoidea blandingi	Graptemys		
Chrysemys picta*	Chrysemys floridana		Chrysemys hibbardi
Chrysemys scripta*	Chrysemys concinna		
		large Hes- perotestudo+	small Hes- perotestudo+
		Gopherus sp.	

¹ E. blandingi and C. picta may be absent during interglacial intervals.

² Habitat preferences uncertain.

* Members of Recent fauna of Meade Co., Kansas.

+ Extinct.

turn out to be occasional (Kanopolis 1.f.) and Kinosternon, possibly did not occur this far east. Terrapene ornata is certainly to be expected.

Holman (1969b) has demonstrated that the known occurrences of (extant) reptiles and amphibians in late Pleistocene deposits of Texas basically conform to Recent distributional patterns as analyzed by Blair (1950) with some notable exceptions. Occasionally, at least, *Alligator* and *Syrrhophus marnocki* ranged northeast or north of their present distributional boundaries.

Large *carolina*-group box turtles, which make their first Quaternary appearances east of Florida and the Atlantic coastal plain during the late Pleistocene, formerly were common in central Texas from north to south and as far west as eastern New Mexico. The large form disappeared entirely, probably by 10,000 yr.; the species *carolina* is now restricted to the eastern third of Texas. Similarly a large, *polyphemus*-like species of *Gopherus* occurred in Texas possibly as recently as the late Wisconsinan of Wheeler Co. and has since vanished.

On the basis of a suggestion made by Bramble (1971), that the small tortoise, Testudo wilsoni Milstead, from late Wisconsinan localities in Oklahoma, Texas, and New Mexico, is related to the large Pleistocene forms of Hesperotestudo (Geochelone of other authors) rather than to the turgida line of small, rugose tortoises, I had hoped to be able to conclude from literature records that wilsoni actually replaced the antecedent large forms in the stratigraphic record. As it turned out, however, the geologic range of H. wilsoni has been extended to ca. 25,000 yr. (Van Devender, in litt., 1977), and a large form lived as recently as a breccia fill in the Longhorn Cavern, Burnet Co., Texas (Semken, 1961). In any case, Hesperotestudo, large and small, together with large Gopherus and carolina-group Terrapene all disappeared during or prior to the interval of extinction of large herbivorous mammals in the Plains region. No other terrestrial or aquatic reptiles or amphibians are known to have undergone extinction or drastic range contractions during this interval in the southern Plains.

Extinction of large *Hesperotestudo* and disappearance of large *Terrapene* occurred also in the southern Mississippi Valley region by the close of the Wisconsinan interval. During the time these forms were extant in the southern states, *Emydoidea* and *Clemmys insculpta* ranged as far south as Mississippi and Georgia, respectively, and *Alligator* lived in Missouri.

SYSTEMATIC LIST OF SPECIES

The order of presentation of turtle families follows that of Gaffney (1975). Recent distributions are taken from Conant (1975), together with information contained in treatments of the known Recent occurrences in individual states (Hudson, 1942; Collins, 1974; Webb, 1970). Shell characters used to determine the various taxa are presented in Appendix A.

Class REPTILIA

Order CROCODILIA

Family Crocodylidae

Alligator cf. A. mississippiensis Daudin

Specimens and occurrence.- In addition to an Ingleside record (Lundelius, 1972), the remaining five Texas occurrences of Alligator (A) shown in Figure 3 include the Slaton l.f. and four later records, from the Moore Pit and Sims Bayou local faunas, and from high terrace deposits at Waco and at Iron Bridge Draw, 50 mi. east of Dallas. The latter occurrence was mentioned in Slaughter et al. (1962). The other four localities were listed by Holman (1969b). Additional, possibly late-Pleistocene, records for Washington and Hays Co.'s are given by Hay (1924). A single tooth (V37173) was found in the Cragin Quarry 1.f. years ago and, to my knowledge, has not been previously reported. It might have been considered a reworked specimen, but since the neighboring and underlying sediments are of late Pliocene or early Pleistocene age (Hibbard and Taylor, 1960), and no alligators are known from this area in deposits of those ages, associating it with the Cragin Ouarry fauna seems reasonable. At least one Missouri record (Herculaneum 1.f.) was noted by Mehl (1962).

Remarks.— As Conant (1975) has pointed out, the correct Recent distribution of the American alligator is impossible to delineate. Except for those from the Slaton, Cragin Quarry and Herculaneum localities, the Pleistocene records are close to known Recent

occurrences of *Alligator*. Along with other faunal elements present, alligators in the Slaton and Cragin Quarry faunas are indicators of a climate and habitat strongly contrasting with the present situation.

Order TESTUDINES Family Kinosternidae Sternotherus odoratus (Latreille)

Specimens and occurrence.— Kanopolis l.f.: material discussed by Holman (1972b); V65874, associated right hyo- and hypoplastra and four additional plastral fragments. Berends l.f.: V60130, right 8th peripheral. Mt. Scott l.f. (UM-K1-60): V61842, nuchal, left hyoplastron, right hyoplastron, left hypoplastron, right xiphiplastron, 27 peripherals and various fragments. Clear Creek l.f.: material discussed by Holman (1963). Brynjulfson Cave No. 2: see Parmalee and Oesch (1972).

Remarks.- The nuchal bone included in V61842 is shown in Figure 4a; the large, thick hyoplastra and hypoplastra are illustrated in Figure 5, along with isolated peripheral V60130. Shape and size of these specimens compare perfectly with material from various Recent populations; however, the detailed remarks by Holman (1972b) regarding the average thickness of the Kanopolis bones relative to Recent specimens apply equally well to the UM-K1-60 sample (V61842). I examined Recent material from Michigan and Texas and found no significant difference in average shell thickness between the northern and southern populations. The Texas specimens may have displayed a more complete degree of ossification between plastral elements in smaller individuals. I continue to hypothesize that shell-bone thickness within species of aquatic turtles is primarily a function of local water chemistry, available diet, and seasonal variations in climate, rather than a reflection of differences in genotype between fossil and Recent populations.



Holman (1975) has moved the earliest recorded occurrence of this species back to the early Pliocene of Kansas. S. odoratus is also known from the late Pleistocene in Florida (see Gehlbach, 1965). The principal western limit of documented Recent distribution of this species is shown in Figure 2 for the Kansas-Oklahoma latitudes (Conant, 1975). The Clear Creek site is near the western boundary of Recent occurrence in Texas at the latitude of Denton Co.

The impression forthcoming from remarks in the natural history literature is that *S. odoratus* has no particular aquatic habitat preference although " it shuns temporary or fluctuating puddles or pools" (Carr, 1952). It is worthwhile to note Cahn's (1937) statement that *Kinosternon flavescens* avoids stream habitats in Illinois: we have no *Kinosternon* remains in the three faunas where *Sternotherus* is well represented.

Kinosternon flavescens (Agassiz)

Specimens and occurrence.- Rezabek l.f.: V33794, right 7th peripheral and fragment. Berends l.f.: V60131, plastron fragments; V33798, carapace parts including 29 peripherals, 1 pygal, 1 suprapygal, nuchal fragment. ?Nye Sink l.f.: KU 7679, fragments. Sloth Locality (UM-K3-61): V61851, right hyoplastron, 4th and 10th peripherals. Cragin Quarry l.f.: V33801, nuchal, 24 peripherals, plastron fragments. Lubbock Lake site: see Johnson (1974). Berclair l.f., Bee Co., Texas: TMM 30924-78, most of left half of carapace with associated nuchal and xiphiplastra.

Remarks.— This material is identical in all respects, including maximum size and average thickness, to shell elements of recent specimens of *K. flavescens.* The nuchal bone included in V33801 is shown in Figure 4C. The probable Nye Sink occurrence is based on Galbreath's (1948) report. I was unable to locate the specimen, and the locality information for KU 7679 was merely "Meade Co., Kansas."

K. flavescens is known from the upper Middle Pliocene of Kansas and Blancan of Kansas and Arizona (Fichter, 1969; see Gehlbach, 1965), and the early Pleistocene of Nebraska and Kansas (Holman, 1972a; Preston, in preparation A). Oddly enough there are no published records of its fossil occurrence in Texas until the Wisconsinan interval. The Recent distribution includes the southern Great Plains southward across the Rio Grande for varying distances into Mexico, and extending westward across Arizona. Relict populations occur to the east, including a differentiated subspecies in central and western Illinois.

This species is associated with permanent or semipermanent bodies of water, large or small, usually with muddy bottoms. It appears frequently in faunas thought to represent interglacial or early or late glacial intervals during the Pleistocene. I can only attribute its scarcity in Texas deposits to lack of suitable local habitat.

Family Trionychidae

Trionyx spinifer Le Sueur

Descriptive characteristics of shell.— So far we have been able to distinguish the species T. spinifer from T. muticus only on the basis of plastron bones. Webb. (1962, p. 474) figured the plastra of the two species; the differences are obvious when consulting this illustration. Holman (1972b) gives a quantitative assessment of the xiphiplastron comparison. Skull bones would be excellent for differentiation; unfortunately the only specimen we have from these faunas is a parietal, with no diagnostic value. To date there are no published fossil records of T. muticus.

Specimens and occurrence. – Kanopolis l.f.: V60485, right xiphiplastron (Holman, 1972b) and epiplastron. Rushville l.f.: UNSM 14835, left hypoplastron. Clear Lake, Sangamon Co., Illinois: see Holman (1966b). Pitt Bridge, Burleson Co., Texas (Hay, 1923); Ingleside l.f., San Patricio Co., Texas (Lundelius, 1972). Most of the Trionyx material from Centipede Cave, Val Verde Co., Texas (Lundelius, 1963) is identifiable as *T. spinifer*.

Figure 4. Nuchal bones or fragments in the UMMP collection from late Pleistocene deposits in southwestern Kansas. (a) Sternotherus odoratus, V61842 (part). (b) Chelydra serpentina, V60084 (part). (c) Kinosternon flavescens, V33801 (part). (d) Terrapene ornata, V56588. (e) Emydoidea blandingi, V57652 (part). (f) Chrysemys (Trachemys) scripta, V61854 (part). (g) Chrysemys (Chrysemys) picta, V60133 (part). (h) Graptemys pseudogeographica or kohni, V65876.



Figure 5. Additional shell bones representing *Sternotherus* odoratus. (a) left hyoplastron (ventral view). (b) right hyoplastron (dorsal view). (c) left hypoplastron (ventral view), Mt. Scott 1.b., UM-K1-60, V61842 (part). (d) right 8th peripheral, Berends 1.b., V60130.

Trionyx sp.

Specimens and occurrence. – Arkalon l.f.: fragments (Preston, 1971). Kanopolis l.f.: fragments (Holman, 1972b); V60997, associated right and partial left hypoplastra, costal. Berends l.f.: V60140, fragments. Sandahl l.f.: V50919, hypoplastron fragment reported by Semken (1966). Butler Spring l.f.: V47663, 64 (see Schultz, 1965); V53895, costal fragment. Mt. Scott l.f. (UM-K1-60): V61848, fragment. XI Ranch (KU Loc. 7): KU 7568, partial carapace (Galbreath, 1948 – locality not given at the time). Clear Creek, Moore Pit, Sims Bayou l.f.'s, see Holman, 1969b. Quitaque l.f., Motley Co., Texas (Dalquest, 1964). Lubbock Lake site (Johnson, 1974).

Remarks.— *Trionyx* remains are usually scarce and fragmentary in late Pleistocene faunas, suggesting, perhaps, that the depositional sites did not include suitable local habitat ("river turtles to a large degree", Conant, 1975). An exception is the Kanopolis 1.f. The genus has a more or less continuous history in the Plains since the early Pliocene.

Family Chelydridae

Chelydra serpentina (Linnaeus)

Specimens and occurrence.- Arkalon 1.f.: see Preston (1971). Kanopolis l.f.: see Holman (1972b). Rezabek 1.f.: V60141, fragments. Berends 1.f.: V60132, fragments. Nye Sink l.f.: V61856, neural fragment, peripheral fragment. Williams 1.f.: V60084, right femur, head of left femur, left ilium, left pubis fragment, nuchal fragment (Fig. 4b), right 10th peripheral. Butler Spring l.f.: V33795, V47660-62 (Schultz, 1965, and additional material collected summer, 1972). Sloth Locality: V61850, right 11th peripheral, fragments. Doby Springs l.f.: V60143, fragments. Mt. Scott l.f. (UM-K1-60): V61841, plastron fragments and caudal ossicle. XI Ranch (KU Loc. 7): see Galbreath (1948). Rushville l.f.: UNSM 14832, peripheral, fragments of humerus. Angus l.f.: UNSM Field No. 2066-53, fragments. Jinglebob 1.f.: V37187, pygal and 5 peripherals. Howard Ranch l.f.: see Holman (1964). Brynjulfson Caves: Parmalee and Oesch (1972). Clear Lake, Sangamon Co., Ill.: Holman (1966b).

Remarks.— The characteristics of chelydrid shell bone that allow identification of fragments are given in Appendix A. *C. serpentina* formerly had a wide distribution as it does now. Permanent water in the vicinity is the only habitat requirement. The species is first recorded in the medial Pliocene (Galbreath, 1948). Van Devender and Tessman (1975) have reported its occurrence in the Pleistocene of Nevada.

Family Emydidae

Terrapene carolina (Linnaeus)

Specimens and occurrence.- Milstead (1967) listed specimens from New Mexico, Texas, Oklahoma, Arkansas, Missouri, Kansas and Illinois. Holman (1969b) also gives a comprehensive list of Texas records. I have indicated the locations of the New Mexico, Texas and Oklahoma occurrences in Figure 3 (TC). T. carolina is also included in the Ingleside 1.f. (Lundelius, 1972), Clear Creek 1.f. (Holman, 1963) and the Lubbock Lake site (Clovis horizon, Johnson, 1974), and two Pitt Bridge localities (Hay, 1924; Milstead, 1967). Additional Missouri records were mentioned above in the annotated list of A complete listing to date of UMMP specifaunas. mens is included below. Slaton 1.f.: V39442, anterior margin of carapace, right epiplastron. Mt. Scott l.f., UM-K2-59: V43474, associated parts of left hyo- and hypoplastron with additional fragments; UM-K1-60: V61843, left xiphiplastron, 2 neurals and peripheral. Cragin Quarry 1.f.: V38637, associated parts of carapace and plastron; V61858, most of forelobe of plastron, additional fragments; SUI 37946, posterior 2/3 of carapace and plastron. Jinglebob 1.f.: V26957 (holotype of T. llanensis Oelrich, 1954), most of carapace and plastron; V57659, left hyoplastron fragment. Sour Lake Pleistocene beds, Hardin Co., Texas: AMNH 3934, in part, epiplastron fragments (holotype of Trachemys trulla Hay, 1908). Trinity River terrace, Navarro Co., Texas: TMM 31071-19, partial hindlobe. The Burnet Cave specimen (ANSP 13809) mentioned in the legend, Figure 3, is a "large, putnami-size T. carolina" (Van Devender, in litt., 1977).

Remarks.— The Slaton, Jinglebob and SUI Cragin Quarry fossils represent large box turtles (greater than 200 mm carapace length). The SUI specimen is 140 mm wide, 78 mm high and 180 mm from the posterior end of the carapace to the anterior seam of the 4th marginal scute. Eshelman (1969) found it to be very similar to V26957 (the Jinglebob specimen, holotype of *T. llanen*sis).

Milstead (1967), on the basis of assumed stratigraphic

relationships of the localities, somewhat arbitrarily called the fragmentary Slaton and Mt. Scott specimens *T. carolina putnami* and referred the Cragin Quarry and Jinglebob material to a position intermediate between *putnami* and Recent *T. c. triunguis*, along with Texas specimens of presumed Sangamonian or early Wisconsinan age. I cannot improve upon Milstead's analysis at this point, but I sense a logical difficulty in synonomizing these relatively young forms with the much older, geographically distant *putnami*, when at the same time they are supposed to be ancestral to one or more Recent subspecies. The difficulty is avoided to some extent by making use of the temporal subspecies concept.

Using some large samples available from local faunas in Texas, however, Milstead (1967) was able to demonstrate a cline in certain characters, leading from large, putnami-like forms in earlier localities, to a merging with the limits of variation displayed by populations of modern T. c. triunguis. New material and stratigraphic refinement reported by Gillette (1974) made it appear that the modern triunguis status had probably been achieved in the Texas populations by about 40,000 yr.; but since the publication of Milstead's analysis and Gillette's refinement, specimens from localities of similar and much younger age have been referred to T. c. putnami (Slaughter, 1975; Moodie and Van Devender, 1977; Van Devender, in litt., 1977). Two possibilities appear to remain. Either (1) the large form was not, in fact, related to T. c. triunguis and simply became extinct, or (2) there was a gradual disappearance of large forms of T. c. triunguis during the Wisconsinan together with a drastic contraction in the range of *triunguis* to the east at or after the close of this interval.

The problem, of course, is not in the analysis supplied by Milstead, whose exhaustive treatment represents the culmination of efforts to date of several workers, but in the lack of good series of fossils from critical ages and geographic areas, as well as adequate stratigraphic knowledge. Milstead (1969, p. 39, p. 64), moreover, anticipated the present ambiguities, and suggested, in more general terms, that the giant form represented one out of three allelic pools postulated to have been existing in latest Pleistocene time. This population has disappeared and left a contribution to the Recent *potpourri* only in the effect of large maximum size in *T. c. major*.

There is no sign of T. carolina in five faunas I have examined from the Blancan interval in the Great Plains.

None of the Pleistocene deposits in Kansas prior to the Mt. Scott have produced any material, and it was not found in the best-studied middle Pleistocene turtle fauna of Texas (Preston, 1966). It could be, then, that the form we are discussing appeared no earlier than the Yarmouthian (if the Slaton 1.f. should be dated at this interval) but no later than late Illinoian time (Mt. Scott 1.f.) on the Plains. Movement was undoubtedly from the east along a mesic corridor, as proposed by Auffenberg and Milstead (1965). That *carolina*-group *Terrapene* was previously a resident of this region is indicated by an early Pliocene record (Holman, 1975).

The large form apparently became established as far north in the Plains as Meade Co., Kansas, and persisted until the Wisconsinan glaciation. In Texas it survived far to the west and to the south of the present distribution of T. carolina triunguis until latest Wisconsinan time (Fig. 3; Milstead, 1967).

Terrapene ornata Agassiz

Specimens and occurrence.- Arkalon 1.f.: V56588, nuchal (Fig. 4d; Preston, 1971). Berends l.f.: V60137, left 4th and V60138, abnormal right 6th peripherals (Fig. 6a,b). Doby Springs l.f.: V60144, left hypoplastron (Fig. 6c) Sloth Locality (UM-K3-61): V61852, partial carapace. Rushville 1.f., Loc. Sh-3: UNSM 14837, 38, most of shells of two individuals, two epiplastra; UNSM 21340, carapace and hindlobe of plastron; 21341, right halves of carapace and plastron; 21342, right xiphiplastron; 21344, right xiphiplastron (Loc. Sh-4). This material was collected by Ray Hintlian. XI Ranch (UM-K2-62): V46069, left hyoplastron; V65877, right hypoplastron (Gopherus locality). Clear Creek 1.f.: Holman (1963). Lubbock Lake site: Johnson (1974). Brown Sand Wedge 1.f.: V57406, most of carapace, and material seen by Milstead (1967).

Remarks.— Based on these and earlier records (see Milstead, 1967) it appears that T. ornata has been a more or less permanent resident of the Great Plains since the medial Pliocene. Since, at latest, the time of the Gilliland 1.f. (Hibbard and Dalquest, 1973), fossils compare more closely with specimens of Recent T. o. ornata than with the fossil subspecies longinsulae. A late Pleistocene record of T. ornata might exist for Missouri (Parmalee et al., 1969). The Coles Co., Illinois, specimen (FMNH P15213) reported by Galbreath (1938) as T. ornata was later identified by Milstead (1967) as T. carolina.



Figure 6. Additional shell bones of *Terrapene ornata*. (a) right 6th peripheral showing indentations of supernumerary scutes, V60138. (b) left 4th peripheral, V60137. (c) left hypoplastron (dorsal view), V60144. (a) and (b), Berends 1.b. (c), Doby Springs l.b.

Emydoidea blandingi (Holbrook)

Specimens and occurrence.— Arkalon 1.f.: V31824, V56500 (Preston and McCoy, 1971), V60573, fragment, V60576, partial carapace, V61012, pygal, V61014, nuchal, 2 peripherals. Nye Sink 1.f.: V61857, right 4th and left 2nd peripherals. Berends, Adams, Doby Springs (Locality 4, Stephens, 1960), Mt. Scott and Jinglebob 1.f.'s: material described in Preston and McCoy (1971). Williams 1.f.: V60089, right 8th and left 11th peripherals and additional fragments. Sloth Locality: V57651, right 9th peripheral. Rushville 1.f.: UNSM 14839, left hypo- and xiphiplastra. XI Ranch (UM-K2-62): V46068, left 2nd and 3rd peripherals. Enon Sink 1.f., Moniteau Co., Mo.: see Preston and McCoy (1971). Brynjulfson Cave No. 1: Parmalee and Oesch (1972). Catalpa Creek site, Clay and Lowndes Counties, Miss.: Jackson and Kaye (1974).

Remarks.— Emydoidea is first recorded in a Rexroadian fauna of the late Pliocene (Preston and McCoy, 1971). It reappears in the Arkalon 1.f. and seems to have a more or less uninterrupted occurrence in the southwestern Kansas area until after the time of the Jinglebob 1.f. The absence of Emydoidea in faunas where turtles are otherwise well represented, such as the Kanopolis, Butler Spring, and Cragin Quarry 1.f.'s is perhaps notable at least in regard to local habitat. A worn peripheral (V57651) was collected at the Sloth Locality, where apparently a marsh habitat existed (Devore, 1975). The specimens from the Nye Sink and Williams faunas represent individuals equal to or exceeding the maximum recorded size in Recent populations (ca. 270 mm). The nuchal bone from UM-K1-60 is shown in Figure 4e.

The comparison between distributions of this species at times during the late Pleistocene and its Recent occurrence is striking (see map in Van Devender and King, 1975). An additional range contraction eastward in the northern part of the distribution is indicated by the Rushville records.

Genus GRAPTEMYS

Graptemys geographica (Le Sueur)

Specimens and occurrence. – Kanopolis I.f.: V60356 (Holman, 1972b). ?Moore Pit I.f., Dallas Co., Texas (Slaughter *et al.*, 1962; Slaughter, 1966; Holman, 1969b).

Remarks.— Graptemys is present in the Oligocene of South Dakota (Hay, 1908 and Clark, 1937), and fossils referable to *G. geographica* occur in three Blancan faunas of the Great Plains (Preston, in preparation B). Due to the irresponsibility of a borrower, the Moore Pit specimen (SMUVP 60109) is apparently lost. It was unquestionably a *Graptemys* (Slaughter, personal communication), but it could have been a sawback (*pseudogeographica* or *kohni*) with worn knobs. The specimen reported from the Trinidad l.f., Henderson Co., Texas, is an excellent *Chrysemys scripta* (Stovall and McAnulty, 1950; Gehlbach, 1965; Holman, 1969b).

Graptemys pseudogeographica or kohni

Specimens and occurrence.- XI Ranch (Gopherus locality): V65876, nuchal fragment (Fig. 4h). Pitt Bridge locality: TMM 40099-55, hyoplastra, left 1st costal and 3rd and 4th peripherals. Batte gravel pit: TMM 41606-1, right xiphiplastron.

Remarks.— The putative species *pseudogeographica* and *kohni* are indistinguishable on the basis of shell characters. It is surprising that more fossil specimens assignable to these species are not known, especially in view of their combined extensive distribution in the central U.S. at present. Range contractions apparently occurred in the northeast at the close of the Pleistocene (see Wilson and Zug, 1966). The Pitt Bridge specimen (Hay, 1923) was reidentified on the basis of short scute overlap on the hyoplastra and a high ratio of shell height to width as compared to that of *Chrysemys concinna* or *floridana* or *C. picta*.

Adult *Graptemys* are molluscivorous and favor larger bodies of water (lakes and rivers) with sufficient vegetation to support the snail portion of their diet.

Genus CHRYSEMYS

The shell characters that separate three subgeneric divisions (McDowell, 1964) of this genus are given in Appendix A. Diagnostic features for individual species of the subgenus *Pseudemys* are presented here in considerable detail to facilitate proper placement of fossil material, including that of an apparently new form.

Subgenus PSEUDEMYS

rubriventris section: Appendix A, Section 18. Except for those from Florida, no fossils are thus far assignable to this section of *Pseudemys*. With respect to epiplastral symphysis length and scute overlap, however, the fossil *C. hibbardi* (see below) is comparable to *C. rubriventris*. I have seen the holotype of *Pseudemys extincta* Hay (NMNH 16678, ?Pleistocene, Hillsboro Co., Fla.) and agree with Hay's (1908) statement that it resembles *C. rubriventris*. Jackson (1976) has clarified the history of *rubriventris* in Florida.

floridana-concinna section: Appendix A, Section 18'.



Figure 7. Chrysemys (Pseudemys) floridana cf. C. f. hoyi, V57663, Arkalon l.f. Above, anterior rim of carapace. Below, forelobe of plastron (ventral view).

Chrysemys (Pseudemys) cf. C. floridana hoyi (Agassiz)

Descriptive characters of shell.- Small (maximum length ca. 300 mm); forelobe of plastron not sharply upturned; moderate notching of posterior peripherals.

Specimens and occurrence.— Arkalon 1.f.: V57663, forelobe of plastron with associated nuchal, anterior peripherals and partial left 1st costal (Fig. 7); V60574, right and left epiplastra.

Remarks.— Considered subjectively, these specimens compare equally well with a *f. hoyi*-like specimen from Waco, Texas, and with *c. heiroglyphica*-like specimens

from Posey Co., Indiana. The length of the epiplastral symphysis and degree of plastral scute overlap (Fig. 8a,b), however, suggest an affinity with *floridana*. Part of the second marginal scute lies on the nuchal bone in V57663. This situation occurred in 20% of the Recent *C. floridana* I examined and in 45% of 9 *C. concinna*. The forelobe of the plastron is slightly concave, a feature associated with *concinna* and *f. hoyi* x *c. heiro-glyphica* hybrid specimens.

Referral of the fossils to recent *C. f. hoyi* is tentative, in part because little "pure" *hoyi* material was available to me for study. The geographical overlap of *hoyi* with *C. c. heiroglyphica* is complete except in central Oklahoma (Conant, 1975) where "pure" *hoyi* might be expected to occur. Likewise, "pure" *heiroglyphica* populations might only be found in the eastern part of the distribution. In 9 adult specimens from Indiana, Mississippi, Tennessee and Louisiana, only one had no evidence of intergrading characters, and that was a *heiroglyphica* from outside the range of *hoyi* (Fig. 8b). The Texas series (Fig. 8) is probably also derived from a hybridizing population, in this case between *C. f. hoyi* and *C. c. texana* (Carr, 1952).

There is a partially developed supernumerary plastral scute on the left side of V57663. Distinct excavations for the deltoid attachments are present on the epiplasta. Measurements of V57663: forelobe length 99, width 93; epiplastron, greatest length 38, width 42; lip width 50. V60574: epiplastron, greatest length 43.5, width 48.5; lip width 47.

The *floridana-concinna* section of the subgenus *Pseudemys* was previously unknown from fossil localities in the Great Plains. A Pliocene form (*Chrysemys williamsi* Rose and Weaver, 1967) from Florida is apparently related to this section of the genus *Chrysemys*. The species *floridana* is known from two late Pleistocene localities in Florida (see Gehlbach, 1965). In the Pleistocene of Kansas, the *floridana-concinna* section is now found in the interval bounded by the Arkalon and Butler Spring local faunas. The Recent distribution of *floridana* and *concinna* extends from the Atlantic coastal plain and peninsular Florida west to the Rio Grande drainage, and in the Mississippi system inland as far north as central Oklahoma and southeastern Kansas in the Plains area (Fig. 2).

The right epiplastron of V57663, collected in 1969, was misidentified and incorrectly reported as *C. scripta* (Preston, 1971). The remainder of the specimen was collected in 1971.



Figure 8. Chrysemys (?Pseudemys) hibbardi, new species. (a) forelobe of plastron, ventral view. (b) same, lateral view. (c) right 9th peripheral. (d) left epiplastron (dorsal view). (a), (b), (c), holotype (part), V33333, Doby Springs lb. (d) paratype (part), V61846, Mt. Scott l.b. (UM-K1-60).

Taxon	Number examined (each side)	Terminatio on 9th peripheral	n % overlap ¹	Termination on 8th peripheral or its posterior suture
Chrysemys j floridana, pennin- sularis	f. 30	2	13,16	28
C. concinna suwannien	sis 12	4	13-38	8
C. tavlori	2	2*	22.25	0
C. ornata	- 14	0		14
C. rubriven- tris, nel- soni	14	5	20-24	9
C. carri (=C. caelat	a) 2	2	20,25	0
C. williamsi	2	0		2*
C. hibbardi	2	2*	19,27	0
C. platymar- ginata ²	- 2	0		2*
C. idahoensi	is 3	3	17,25*,25*	0
C. hilli ²	2	0	_	2*
<i>Graptemys</i> sp.	46	0		46
G. inornata	2	0		2*
G. cordifera	2	0		2*
Echmatemy septaria	s 2	2*	25,25	0
Echmatemy remaining species	s, 24	0		24

 TABLE 3.
 Position of distal end of third interpleural sulcus in selected emydid turtles.

* type specimen.

¹ measured along pleural-marginal sulcus on 9th peripheral.
² pleural-marginal sulcus overlies costal-peripheral suture as in most C. scripta.

Chrysemys (Pseudemys) cf. C. concinna heiroglyphica

Descriptive characters of shell.- Large (max. 370 mm); forelobe of plastron very flat or slightly concave; shell bones relatively thin compared to those in coastal plain populations; posterior peripherals moderately notched and conspicuously horizontally-projecting; shell occasionally narrowed in region of 6th marginals, or 5th and 6th peripheral bones (Carr, 1952).

Specimens and occurrence.— Butler Spring 1.f.: V61855, right 1st, left 8th and 11th peripherals, 2 partial 1st neurals.

Remarks.— Most of the bones represent large individuals. One of the neurals is from a turtle close to known maximum size for *heiroglyphica*. The posteriomedial corner of the second marginal scute is in contact with the nuchal as shown by the seam impressions on the first peripheral. The posterior peripherals are thin and flat compared with the same bones from *C. scripta*. The neurals display no trace of median longitudinal keel.

It is primarily on the basis of greater size that these specimens are distinguished from the Arkalon material. The river habitat implied by the Butler Spring aquatic fauna (Schultz, 1965) further justifies the comparison with C. concinna, a predominantly river-inhabiting species.

One of the peripherals under V60355, a left 8th, reported by Holman (1972b) from the Kanopolis local fauna should not be referred to *C. scripta* and probably represents *C. concinna* (Table 1). A right 1st peripheral included in TMM 30965-18, from the Berclair 1.f., Bee Co., Texas, possibly belongs to *C. concinna*.

Chrysemys (?Pseudemys) hibbardi, new species

Diagnosis.— An extinct Chrysemys of moderate (ca. 300 mm) maximum size, provisionally referred to the floridana-concinna section of subgenus Pseudemys; forelobe of plastron very flat and broad; epiplastral symphysis very long (Fig. 8a); humeral scute overlap similar to that of floridana or floridana x concinna hybrids (Fig. 8b); epiplastral lip width characteristic of concinna (Fig. 8c); attachment area of deltoid muscle on epiplastron extensive and very shallow; 3rd interpleural seam contact in far posterior position on 9th peripheral in type (Table 3); posterior peripherals faintly notched or not at all. Skull, cervical vertebrae, nuchal, pygal, xiphiplastron unknown.

Specimens and occurrence.- Holotype, V33333, forelobe of plastron (Fig. 9a) with associated 9th (Fig. 9c) and left 11th peripherals and pleural fragments, from Mrs. L. Dees' Ranch, N½ SW¼ Sec. 10, T 27 N, R 24 W, Harper Co., Oklahoma, Doby Springs local fauna, Locality 2 (Stephens, 1960); collected by Claude W. Hibbard and University of Michigan field party, summer, 1955. Paratype, V61846, left epiplastron (Fig. 9d) and 10th peripheral fragment, from the Big Springs Ranch, SW¼ SW¼ Sec. 13, T 32 S, R 23 W, Meade Co., Kansas, Mt, Scott local fauna, locality UM-K1-60 (Hibbard, 1963b); collected by Hibbard and party, summer, 1961.

Remarks.— Both type and paratype specimens are from adult individuals estimated to have had carapace lengths of 250 mm. The carapace is not sculptured. The posterior peripherals are not strongly curved and probably projected obliquely downward. The right 10th peripheral (V61846, in part) displays very little or no notching at the apex of the intermarginal seam. The emergence of the rib head on a costal fragment is close to the central end of the bone. The right 9th peripheral of the type has the seam between the 3rd and 4th pleural scutes meeting the pleural-peripheral seam at a position more than 25% of its anterior-posterior length (Fig. 9c, Table 3).

Apart from the greater length of the epiplastral symphysis, and differences in the deltoid muscle-attachment area, the epiplastron resembles closely that of concinna in the floridana-concinna section of Chrysemys. At sight, the most arresting difference is the much greater size of this bone compared to those from similarsized specimens of concinna, suggesting an anterior and lateral expansion of the element without the corresponding development of a raised, thickened epiplastral lip as in C. rubriventris and scripta. The epiplastra were also compared with those in a series of 7 C. ornata, in which the relative epiplastral symphysis length turned out to be similar to that in the floridana-concinna section (maximum % of forelobe length 19.5). The entoplastron is bell-shaped in ventral aspect, with a constriction at the gular-humeral seams. This condition is seen frequently in Chrysemys but not in Graptemys where the entoplastron has a simpler, more quadrangular shape. Fine ridges are evident on the lateral surface of the hyoplastron in the axillary region.

Rose and Weaver (1966) described *Chrysemys williamsi* from the Pliocene of Florida, and discussed the affinities of this form with Recent *C. floridana* and *concinna. C. hibbardi* is similar in regard to the smooth carapace and lack of notching of posterior peripherals. From the published description, however, it is clear that *C. williamsi* has a shorter plastral scute overlap than C. hibbardi. In addition, the forelobe of the plastron in C. williamsi is upturned and the distal end of the 3rd interpleural seam is on the 8th peripheral. I have encountered no fossil forms from the Plains thus far that might be ancestral to C. hibbardi.

This species is known only from the Doby Springs and Mt. Scott local faunas (Pleistocene; Illinoian), Harper Co., Oklahoma and Meade Co., Kansas, respectively.

Subgenus TRACHEMYS

Chrysemys (Trachemys) scripta (Schoepff)

Descriptive characters of shell.— As for subgenus (see Appendix A, Section 19).

Specimens and occurrence.- Arkalon 1.f.: V48000, V56587 (Preston, 1971), V61013. Kanopolis 1.f.: V60355, in part (Holman, 1972b; see comment above under Chrysemys cf. C. heiroglyphica). Berends 1.f.: V60136, nuchal. Adams l.f.: V32447, 2 peripherals, pygal. Butler Spring 1.f.: V47684-85, V47757 (Schultz, 1965); V60010, plastron parts, and V61854, carapace parts (nuchal shown in Fig. 4f). Sandahl l.f.: V50945-46 (Semken, 1966). Williams 1.f.: V60088, peripheral fragments, epiplastron. Angus l.f.: UNSM uncat., carapace and plastron parts. Doby Springs l.f. (Locality 2, Stephens, 1960): V65873, pygal. Mt. Scott 1.f. V61845, nuchal, peripherals, costal (UM-K1-60): fragments. XI Ranch localities: V46051, right 7th and 8th peripherals (UM-K2-62). V29027, hyoplastron, 2 hypoplastra; KU 4703; peripherals and right hypoplastron; KU 25269, nuchal (KU Loc. 7). Clear Creek and Sims Bayou local faunas (see Holman, 1969b). Sour Lake deposits, Hardin Co., Texas: AMNH 3934, in part, right hyo- and hypoplastra, left xiphiplastron (holotype of Trachemys trulla Hay, 1908); AMNH 3933, epiplastra (holotype of Emys petrolei Leidy, see Hay, 1908, p. 352). ?Late Pleistocene, Atascosa Co., Texas: ANSP ?uncat., part of carapace (?part of holotype of Pseudemys bisornatus Cope, see Hay, 1908, p. 353). Berclair 1.f., Bee Co., Texas: TMM 31048-13, left hyoplastron. Trinidad 1.f. (Boatwright pit), Henderson Co., Texas: TMM 30907-62, plastron and partial carapace (see remarks under Graptemys geographica). Batte gravel pit, Milam Co., Texas: material included under TMM 41591-7. Ingleside 1.f., San Patricio Co., Texas (Lundelius, 1972). Berclair l.f., Bee Co., Texas: TMM 31048-13, left hyoplastron. Trinidad l.f. (Boatwright pit), Henderson Co., Texas: TMM 30907-62, partial carapace and plastron (see remarks under Graptemys



geographica). Batte gravel pit, Milam Co., Texas: material included under TMM 41591-7. Lubbock Lake site (Johnson, 1974). Jones Spring l.f. (Moodie and Van Devender, 1977). Clear Lake, Sangamon Co., Ill. (Holman, 1966b).

Remarks.- Upon examination of the holotype of Trachemys trulla Hay it was found that the epiplastra, the peculiarities of which Hay used to distinguish the specimen from typical Chrysemys (Trachemys) scripta and other fossil Trachemvs, actually represent Terrapene carolina. The remaining bones under AMNH 3934 are clearly referable to C. (Trachemvs) scripta. Weaver and Robertson (1967) have included all late Pleistocene (Rancholabrean) Chrvsemvs (Trachemvs) under the designation Chrvsemvs scripta petrolei, a matter I discussed earlier (Preston, 1971). Hay (1908) believed the epiplastra of *petrolei* to be distinct from any of the recent forms of Trachemys, but the referred nuchal bone clearly belongs to scripta. Formal synonomy still requires examination of the *petrolei* epiplastra, but the outcome will probably be that the three forms described from Texas, petrolei, bisornata, and trulla are conspecific with Chrysemys (Trachemys) scripta. It is perfectly reasonable to give them all the subspecies designation "petrolei" as long as they are from a region restricted enough that geographic isolation is not a possibility; however, as I mentioned previously (Preston, 1966), the population from the earlier Gilliland 1.f. is identical, except for shell thickness, to Recent C. (T.)scripta elegans.

C. (Trachemys) scripta has been present in the Great Plains since, at least, the time of the Beck Ranch local faunas (Rogers, 1976). None of the late Pleistocene fossil occurrences are markedly outside the Recent limits of distribution. The species *scripta* is known from the late Pleistocene of Florida (see Gehlbach, 1965). Its occurrence in an assemblage containing jackpine (Moodie and Van Devender, 1977) is of interest. The presence of C. (T.) scripta in a fauna implies a nearby aquatic habitat consisting of quiet water and containing some vegetation.

Subgenus CHRYSEMYS

Chrysemys (Chrysemys) picta (Schneider)

Descriptive characters of shell. As for subgenus (see Appendix A, Section 19').

Specimens and occurrence.- Arkalon 1.f.: V56586 (Preston, 1971); V60575, most of plastron and fragments; V61015 right 11th peripheral, pygal. Rezabek 1.f.: V60142, left epiplastron and fragments. Berends 1.f.: V60133 (nuchal in Fig. 4g) carapace and plastron parts. Butler Spring 1.f.: V29978, V47686-88 (Schultz, 1965). Sloth Locality: V45872, carapace and plastron parts. Williams 1.f.: V60085, nuchals and epiplastra; V60086, carapace parts; V60087, plastron parts; V60577, 7th cervical vertebra. Angus 1.f.: UNSM uncat., carapace and plastron parts. Hay Springs 1.f.: PU 10853, shell (holotype of Chrysemys timida Hay, 1908). Rushville 1.f.: UNSM 14831, carapace and plastron parts; 21342, right hyoplastron; 21243 right xiphiplastron. Doby Springs 1.f. (Locality 2, Stephens, 1960); V60145, carapace and plastron parts. Mt. Scott 1.f.: V61844, nuchal fragments, right epiplastron, carapace and plastron parts (UM-K1-60); V61849, peripherals, neurals, entoplastra (UM-K2-59). XI Ranch (KU Loc. 7): V61859, KU 6479, KU 7569, carapace and plastron parts. Jinglebob 1.f.: V56779, most of shell. Lone Tree Arroyo,

Figure 9. Analysis of selected plastral characters in Graptemys and Chrysemys (Pseudemys), with the corresponding ratios obtained from V33333 (holotype) and V61846 (paratype) of Chrysemys hibbardi as well as from V57663 and V60574, Chrysemys cf. C. floridana hoyi, Arkalon l.f. (a) Length of epi-epiplastral suture, measured on the ventral surface of the plastron, x100 and divided by the forelobe length (length of plastron from hyo-hypoplastral suture to anteriormost part of epiplastral lip). Note long epiplastral symphysis of Chrysemys hibbardi. (b) Length of gular-humeral sulcus on dorsal surface of plastron (overlap of humeral scute) x100 and divided by width of epiplastral lip in the case of Chrysemys floridana and the Arkalon specimens. In the remaining recent populations and C. hibbardi, the overlap/lip width ratios are multiplied by the ratio of the mean of the lip width/forelobe length ratio in the population to that in *floridana*, thus relating all the overlap data to a lip width characteristic of the *floridana* population. Note degree of overlap of the Arkalon C. cf. floridana compared to the recent specimens, and the short overlap in the C. concinna suwanniensis examples. UMMZ 99229 is a C. c. heiroglyphica from Humphreys Co., Tenn., extralimital to the C. f. hoyi population. The low ratio in UMMZ 101754 is due to a wide epiplastral lip; the scute overlap is greater than any of the "pure" concinna. UMMZ 114040 was identified as C. f. hoyi. The remaining Chxh, all within one SD_{n-1} of the mean, had both heiroglyphica and hoyi characters. (c) Variation in width of epiplastral lip expressed as the percent width of the plastron measured at the epi-hyoplastral sutures. Long vertical lines = means, horizontal lines = ranges, open bars = SD_{n-1} of means of ratios indicated. Gp/k: Graptemys pseudogeographica ot kohni. Gg: G. geographica. Ccs: Chrysemys concinna suwanniensis; Chxh: C. c. heiroglyphica x hoyi; Texas: C. floridana x concinna, Central Texas; Cf: C. floridana ssp., Florida and Georgia; Cr/n: C. rubriventris and nelsoni.

Meade Co., Kansas: V26370, costal. Jones 1.f.: V56338, V56490 shell fragments. Brynjulfson Cave No. 2 (Parmalee and Oesch, 1972).

Remarks.— The 7th cervical centrum in emydids and testudinids is normally amphicoelous; specifically, the articulations are double and concave at both ends. V60577, however, has one convex and one concave articular facet anteriorly: an "asymmetrical double joint" (Williams, 1950a). Williams found this condition in 2 out of 195 cervical series of *C. picta* that he examined.

It might be possible to investigate relationships of these fossils to Recent subspecies on an osteological basis, but so far no attempt has been made to do this. All of the records are from localities within the range of Recent C. (Chrysemys) picta belli. The southwestern Kansas-Oklahoma Panhandle localities are at the margin of the principal C. picta range. Fossils identifiable as C. picta are found as early as the upper middle Pliocene of southwestern Kansas (Preston, in preparation A). The species occurs in Blancan (?early Pleistocene) faunas of Nebraska (Holman, 1972a), Kansas (Preston, in preparation A) and Blancan to early Irvingtonian faunas of Texas (Rogers, 1976; Preston, in preparation A). I have reassigned a specimen from a Pitt Bridge locality (Burleson and Brazos Co.'s, Texas; Hay, 1923) to Graptemvs (see section on Graptemvs above).

Specimens of *C. picta* from some of the faunas, notably the Sloth Locality and the Angus local fauna, display prominent, widely-spaced seasonal growth marks. In these same assemblages are found, in abundance, large specimens of *Chrysemys (Trachemys) scripta*. Superficially, the implication is one of conditions conducive to rapid growth and high population density. It should be of interest to attempt a comparison of relative growth rates of *C. picta* in the various faunas in which sufficient numbers of specimens occur.

Family Testudinidae

Each of the two genera in the new-world division of this family that occur in late Pleistocene faunas present nearly insurmountable nomenclatural problems at the species level. In the case of *Gopherus* it is true that the Pleistocene fossils most closely resemble Recent *G. polyphemus* but there is reason to believe the Pleistocene Florida and Great Plains *Gopherus* were different species on zoogeographical grounds. A discussion of alternatives for naming the presumably extinct Great Plains form will be given below.

I have followed Bramble's (1971) concept of the genus Hesperotestudo, and have followed Auffenberg's (1962b. 1963, 1974) proposed continuation of the small turgida line into the late Pleistocene of the Plains. Hesperotestudo equicomes is considered a valid species, although new material assignable to it has shown a relationship to the large forms (campester or crassiscutata) rather than to the series of small, rugose tortoises (turgida line, Auffenberg, 1963). The large specimens from Sangamonian and Wisconsinan localities in Texas are designated "species A"; they are probably related to A small tortoise occurring in the H. crassiscutata. Arkalon and Berends local faunas is called " species B." H. wilsoni, from Wisconsinan sites in Oklahoma, Texas, and New Mexico, is considered a valid name, although its relationship is possibly with the larger species (Bramble, 1971).

Gopherus sp.

Definition.— A large, extinct Plio-Pleistocene species of Gopherus (for definition of genus see Bramble, 1971; Auffenberg, 1974; Williams, 1950b) occupying the southern Great Plains and Central Lowlands physiographic provinces (Fenneman, 1931). Except for apparently much greater maximum size, similar to Recent G. polyphemus. In all specimens of the anterior end of the plastron that I have examined, the intergular sulcus is shorter than the interhumeral. A typical plastron is figured in my 1966 paper.

Descriptive characters of shell.- See Appendix A, Section 20.

Specimens and occurrence.- Arkalon 1.f.: V57043, V57662, pygal (Preston, 1971). Nye Sink: V32450, parts of carapace; V65875, left first peripheral; KU 7677, pleural and neural fragments (Galbreath, 1948). XI Ranch localities: V45639, peripheral and left hyoplastron fragments, ilium; V47716, scapula, proximal half of tibia; V61019, right epiplastron fragment (KU Loc. 7). V29027, carapace and plastron, and V29032, associated skull; V42248, fragments V42249, 2 costals, neural, shaft of right femur; V46085, part of plastron; V46093, right pubis; V61662, costal (Gopherus locality and UM-K3-59). Ingleside 1.f.: TMM 30967-1817, shell (Auffenberg, 1962a; Bramble, 1971; Lundelius, 1972). Wheeler Co., Texas, PPHM P40-1, shell (Auffenberg, 1962a; Bramble, 1971); gravel pit, Haskell Co., Texas: TMM 40473-5, complete shell. See map, Figure 3 (Goph) for Texas localities. The following specimens are from unnamed localities of uncertain stratigraphy: Atascosa Co., Texas: ANSP 9791-94 (cast V31430, holotype of *Testudo atascosae* Hay. See Hay, 1908). Harper Co., Kansas: KU 5935, pleural fragment (Galbreath, 1948). Meade Co., Kansas: V32451, worn peripheral and distal end of ulna: V46063, fragments (XI Ranch, above caliche, basal Qs₂ of Hibbard and Taylor, 1960, SE¼ SW¼ Sec. 33, T 34 S, R 29 W).

Remarks.- Since lost or fragmentary type material does not permit comparison with newly-collected specimens from the same fauna or between faunas of different ages, synonomizing becomes difficult. It is a matter of (1) discarding all species names based on inadequate type material, (2) redefining (or synonomizing) a species based on more complete specimens from the same local fauna or at least from a neighboring stratigraphic and geographic location, or (3) using species names arbitrarily to indicate temporal horizons, hoping there might be some fortuitous biological significance inherent in this procedure. Of the two latter viable alternatives the first is obviously the ideal course to follow; it simply being a question of how long it will take to accumulate the necessary additional specimens. In my opinion it has already been done in the case of late Pliocene or early Pleistocene, Blancan, Gopherus from the equivalent Blanco and Cita Canvon local faunas. Thus G. canvonensis should be in the synonomy of G. pertenuis (Cope, 1892), a possibility suggested by Auffenberg and Milstead (1965) and restated by Bramble (1971). Additional material from the period can then be assigned to G. pertenuis by comparison with specimens of canyonensis.

Two species names are available for Gopherus from the Irvingtonian, early Pleistocene Rock Creek local fauna, Briscoe Co., Texas. Of these, G. laticaudatus (Cope, 1893, p. 75) has priority by page over G. hexagonatus (Cope, 1893, p. 77). Since examining the type material of laticaudatus, I agree with Auffenberg (1974) that it belongs to Gopherus. A redescription of the Rock Creek Gopherus was undertaken by Auffenberg (1962a); however, for replacement material he used specimens from two widely separated late Pleistocene localities. Among other features the size of the type specimen of G. hexagonatus, in comparison with the length apparently attainable by Pleistocene Gopherus, indicates that it was an immature individual. The resulting confused picture of what G. hexagonatus really is has led Bramble (1971) to consider the possibility

that this form belongs to his genus *Scaptochelys* and may be ancestral to Recent *S. berlandieri* and *agassizi*. In this context it should be noted that one of Auffenberg's referred specimens is from within the range of Recent *S. berlandieri* (Ingleside locality). Bramble, however, has since informed me that he no longer regards *hexagonatus* to be a species of *Scaptochelys*.

The above arguments lead to the following possible simplification in species nomenclature for Pleistocene *Gopherus*:

Blancan: G. pertenuis (Cope, 1892) (=G. canyonensis Johnston)

Irvingtonian: G. laticaudatus (Cope, 1893) (=G. hexagonatus Cope, 1893) (?=G. atascosae Hay)

Rancholabrean: G. sp. (this report) (?=G. atascosae, ?=G. polyphemus)

Hibbard (1970) suggested that the Arkalon local fauna of Seward Co., Kansas was equivalent to the Rock Creek local fauna, in which case the Arkalon specimens could be assigned to *G. laticaudatus* in this scheme.

Despite the simplifications offered here and by Auffenberg and Milstead (1965), the idea of retaining species names purely on the basis of stratigraphic and faunal association seems highly artificial. Based on my experience with fragmentary, but suggestive, Gopherus material dating from the Saw Rock Canyon and younger faunas of Kansas and the early Pleistocene of the Plains region in Texas, I think it likely that all of it belongs to a single extinct species occupying at least the entire southern Great Plains. The specimens in all cases indicate a close relationship to Recent G. polyphemus except for greater maximum size. Although frequent gene exchange with a Florida-Gulf Coast population is a matter of high probability during intervals in the Pleistocene (Auffenberg and Milstead, 1965), the fact of some degree of isolation and the apparent temporal as well as geographic morphological uniformity of the Great Plains population argue strongly for a separate species designation. Curiously, there are no published records of the occurrence of Gopherus in Florida prior to the late Pleistocene. It might turn out that the modern polyphemus population is a displaced relict, occupying a Gulf Coast refugium, of the Pleistocene Great Plainscentered species (Auffenberg and Milstead, 1965). These remarks do not apply to Bramble's (1971) Texas Hemphillian species, G. hutchisoni, where the shell is described as "relatively thick". Another possible exception is a partial plastron (U. of California 43274) reported by Brattstrom (1961) from the Cita Canyon area. In this specimen the intergular-interhumeral seam length ratio is characteristic of G. flavomarginatus.

Of the five specimens I regard as dating from late Pleistocene time in Texas, two are from localities older than 50,000 yr. and three are from localities for which no dates are available. *Gopherus* may have undergone relatively early extirpation on the Plains.

Genus HESPEROTESTUDO

Definition.— The characters used by Williams (1950b) and Bramble (1971) are abstracted in Appendix A, Section 20'.

Remarks.— Bramble (1971) has convincingly argued that (Old World) *Geochelone* has no representatives in the Western Hemisphere. Therefore the name *Hesperotestudo*, erected by Williams (1950b) for Nearctic, later Cenozoic members of his collective genus *Geochelone*, is considered a generic designation by Bramble. This usage is followed here.

During the Pliocene two forms with modified caudal vertebrae and a supracaudal "buckler," consisting of a shallowly convex plate of firmly co-sutured dermal bones, inhabited the Plains area (subgenus Hesperotestudo, Auffenberg, 1963). A larger (carapace length up to 1,000 or larger) form, H. campester, persisted at least until the early Pleistocene of Texas (Holman, 1969b; Auffenberg, 1974). A series of smaller forms (carapace length 300 or less) also persisted at least until the early Pleistocene of Nebraska (Auffenberg, 1963; Holman, 1972a; Rogers, 1976). The shells of these forms (turgida line, Auffenberg, 1963) are usually proportionately very thick and the exterior deeply sculptured, or rugose, in contrast to those of adults of the larger lineage. Specimens possibly referable to the turgida line are termed "species B" in the following discussion.

Preliminary comparisons of new material assigned to *H. equicomes* (Hay) with specimens of *H. campester*, members of the *turgida* line, and *H. crassiscutata* (from Florida) show that *equicomes* is probably a valid species and that it is related to one of the large forms (Preston, in preparation C). Shells or fragments of large *Hesperotestudo* from the late Pleistocene of Texas are assigned to *H. crassiscutata* by Auffenberg (1974). Since it now

appears possible that these large Texas specimens might be related to H. equicomes, I have called them "species A" in the following list.

Hesperotestudo equicomes (Hay)

Definition.— Provisionally, a medium to large-sized Hesperotestudo known from the Sangamonian Cragin Quarry 1.f. of Meade Co., Kansas (original description in Hay, 1917).

Specimens and occurrence.— Cragin Quarry 1.f.: NMNH 10944 (cast, V31427; holotype), right epiplastron and left hyoplastral fragment, probably of an immature individual; KU 4899, partial carapace and plastron, limb bones and dermal ossicles; V37172, left humerus; V38640, dermal ossicles from limb armor.

Remarks.— A more complete description of the Cragin Quarry material is postponed (Preston, in preparation C). V38640 was identified as a partial supracaudal buckler by Auffenberg (1962b), but I am certain it represents instead a nearly complete plate of limb armor as can occur in Auffenberg's (1963) subgenus *Caudochelys*.

Hesperotestudo, species A

Definition.— A large, relatively smooth-shelled tortoise occurring in Sangamonian-Wisconsinan local faunas in Texas (Hsp., Fig. 3). Caudal structure and armor unknown.

Specimens and occurrence.- Moore Pit 1.f. (Second Trinity River Terrace, Hill Gravels member (Slaughter, V34554, complete shell (figured in *et al.*, 1962): Hibbard, 1960). Fragmentary material assignable to species A has been found in the Ingleside, Easley Ranch, Clear Creek, and Sims Bayou local faunas of Texas (Holman, 1969b; Lundelius, 1972). Additional, probably late Pleistocene material was previously described by Hay from these Texas localities: Sour Lake, Hardin Co. (Hay, 1924); second terrace, Brazos River near Waco, McLennan Co. (Hay, 1916); Pitt Bridge, Burleson Co. (Hay, 1916, 1923; Auffenberg, 1974); Trinity River terrace at Carrollton, Dallas Co. (Hay, 1923) and a possible occurrence in Washington Co. (Hay, A very late record probably occurs in the 1924). Longhorn Cavern of Burnet Co., Texas (Semken, 1961). A large tortoise (cf. crassiscutata) was reported from the Catalpa Creek site in Mississippi (Jackson and Kaye, 1975).

Remarks.- V34554 has a carapace length of 1100

mm. "Surface float" specimens of large tortoises (e.g., V42250, V61007) are occasionally found at fossil localities in Kansas. These are invariably worn fragments of shell and cannot be regarded as indicators of occurrence in a fauna. I have left these out of the discussion but intact in collections.

Hesperotestudo, species B

Definition.— See Oelrich (1957) and Bramble (1971). Maximum length 300 mm. Shell usually very thick and rugose. Anterior peripherals much longer (proximaldistal dimension) than wide (circumferential dimension).

Specimens and occurrence.— Arkalon 1.f.: V47999 associated right 9th, 10th and partial 8th peripherals and V56589, right 3rd peripheral (Fig. 10a). Berends local fauna: V60139, peripheral.

Remarks.— These specimens apparently represent mature, small, thick-shelled tortoises; the rugosity and thickness are similar to that seen in Pliocene *H. turgida* and *riggsi* material. The posterior peripherals, however, are proportionally somewhat shorter in the proximal-distal dimension compared to *H. riggsi*.

Bramble (1971) has confirmed Oelrich's (1957) contention that the type of Geochelone johnstoni (Auffenberg, 1962b) is actually a juvenile of the large Hesperotestudo that occurs in the Blancan Cita Canyon local fauna of Texas. My designation, "Geochelone cf. G. johnstoni" (Preston, 1971), for the Arkalon specimens is thus inappropriate. The unusually thin-shelled tortoise (V46787) possibly belonging to the turgida series from the Gilliland local fauna, which must now be considered early Pleistocene (Hibbard and Dalquest, 1973), has also previously been called "johnstoni" (Hibbard and Dalquest, 1966; Holman, 1969b). With the exception of the basal Pleistocene Sand Draw local fauna (Holman, 1972a), these presumed representatives of the turgida series are uncommon in Pleistocene localities in the Plains region. If Hesperotestudo wilsoni and the Cragin Quarry specimens are correctly regarded as members of the campester or crassiscutata lineages, the Berends specimen represents the last known occurrence of the turgida line in the Great Plains.

Hesperotestudo wilsoni (Milstead)

Definition.- According to Milstead (1956) "small size, carapace elliptical, sixth through eighth neurals hexagonal, pleural plates arranged in a series of alternat-



Figure 10. Peripheral bones of *Hesperotestudo* sp. Left, V60378, Kanopolis l.f., left 3rd. Right, V56589, Arkalon l.f., right 3rd.

ing wedges, marginal scutes fully as wide as the peripheral bones, epiplastral lip abruptly projecting from the margin of the plastron but not reaching beyond the edge of the nuchal, epiplastral lip notched but not deeply forked, gulars extending for a short distance on to the epiplastron ... anal scutes quadrangular, and xiphiplastral notch broad and deep."

Occurrence.— Friesenhahn Cave I.f., Bexar Co., Texas (Milstead, 1956); Domebo I.f., Caddo Co., Oklahoma (Slaughter, 1966b); Brown Sand Wedge I.f., Curry Co., New Mexico (Slaughter, 1975). Radiocarbon dates for these faunas indicate an average age of 11,000 yr.

Remarks.— Opposing points of view regarding the ancestry of this form have been mentioned earlier in the discussion. Moodie and Van Devender are currently studying the specimens that have been referred to the species wilsoni and their temporal and geographic distribution. Evidence to date indicates that the extinction of H. wilsoni took place in the interval between the Clovis and Folsom cultural horizons, and contemporaneously with the disappearance of carolina-group box turtles from New Mexico and western Texas.

Hesperotestudo, species undetermined

Specimens and occurrence.- Kanopolis 1.f.: V60378,

left 3rd peripheral (Fig. 10); V60379, neural. Angus l.f.: UNSM 14835, partial shell, including nuchal and xiphiplastra, of immature individual. Estimated lengths of carapace and plastron 306 and 291, respectively. Cervical scute length 17, width 15. Nuchal 68 wide; maximum thickness 14. Xiphiplastron width 50, midline length 52. Anal notch shallow. Quitaque l.f., Hall Co., Texas: Midwestern State University VP 1143, peripheral (Dalquest, 1964).

Remarks.— In all probability the Angus specimen is referable to *H. equicomes*. The Kanopolis peripheral is proportionately longer (anteroposterially) than the corresponding bone in members of the *turgida* series. The octagonal neural is 6-7 mm thick and smooth surfaced. These two occurrences are noted as "*Hesperotestudo*, species A" in Table 1.

Summary

Distributional patterns for the turtles and alligator were summarized at the end of the faunal discussion. New and currently complete listings of the turtle segments are given in Table 1 and in the faunal discussions for the Rezabek, Berends, Doby Springs, Williams, Sloth Locality, Mt. Scott, Rushville and Angus local faunas. Additions have been made to most of the remaining localities in Kansas.

Previously unreported late Pleistocene occurrences in Nebraska, Kansas, Oklahoma or Texas are given for the following species: Kinosternon flavescens, Graptemvs pseudogeographica. Chrvsemvs concinna. C. floridana and, probably Alligator. C. floridana and C. concinna are distinguishable on the basis of shell characters and were apparently distinct from each other during the early part of the late Pleistocene. The Chrvsemvs floridana in the Arkalon 1.f. is best compared with Recent C. f. hoyi. Either the Arkalon form was fortuitously very similar to hovi or this race was distinct as early as 0.6 x 10⁶ yr. ago. An apparently extinct aquatic emydid, Chrysemys hibbardi probably was also a member of the floridana-concinna section. Perhaps it was a northern form whose viability and fossil record, in large part, did not survive the severity of Wisconsinan glaciation.

All other late Pleistocene material representing the Emydidae is clearly assignable to Recent species. Terrapene carolina, however, reached a much greater maximum size during much of the period than it does in any Recent population. Shell thickness greater than the average for Recent populations is found in fossil Sternotherus (Kanopolis, Mt. Scott local faunas) and in some of the Terrapene ornata material (Arkalon, Doby Springs). Carapace-length estimates of some specimens of Emydoidea (Nye Sink, Williams) may exceed the known maximum for Recent populations. The Arkalon T. ornata nuchal is very large. The ornata specimen from the Sloth Locality is identical with Recent T. o. ornata and is distinct from T. ornata luteola (see Milstead, 1967).

The complete shells of Gopherus that I have seen compare best with Recent G. polyphemus although, in general, Pleistocene Gopherus reaches a much greater size than the known maximum for polyphemus. My view is that large Pleistocene Gopherus from the Great Plains region which display affinities to G. polyphemus as opposed to G. flavomarginatus belong to a single extinct species. The nomenclatural problems posed by previous descriptions of fragmentary type material were discussed above. At this point only a large amount of complete skeletal material from several intervals during the Pleistocene will prove or disprove any contention.

With the Angus fossil the geographic range of Hesperotestudo is extended to southern Nebraska for the late Pleistocene. I have divided the fossil material which is not sufficiently complete for assignment to described species into two groups, which are distinguished principally on the basis of adult size. The smaller form, probably belonging to Auffenberg's turgida line, persisted in southwestern Kansas until the time of the Berends l.f. Additional material from the Cragin Quarry 1.f. shows that the species H. equicomes is not a member of the turgida line, but is, instead, a large, smoothshelled tortoise. I have not been able, so far, to advance the understanding of the relationships of the giant tortoises that persisted into the Wisconsinan stage throughout the southern United States. Auffenberg's (1974) suggestion that they are all representatives of H. crassiscutata will probably prove to be correct.

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APPENDIX A

A key to the identification of turtle shell bones occurring in late Pliocene and Pleistocene deposits of the Eastern and Central United States

This key is a preliminary effort and much improvement can be expected in its content and construction over the course of time. As it stands only one species of *Sternotherus* is represented. Further characters for *Sternotherus* are given by Holman (1975).

I have not studied the Mexican forms assigned to *Chrysemys scripta* adequately enough to include them. I have dealt with only two species of *Graptemys*.

Many of the diagnostic characters have been abstracted from published work; e.g., Hay, 1908; Tinkle, 1962; Webb, 1962 (*Trionychidae*); Milstead, 1969; Moodie and Van Devender, 1977 (*Terrapene*); Weaver and Rose, 1967 and Adler, 1968 (*Chrysemys*); Wilson and Zug, 1966 (*Graptemys*); Williams, 1950b, Auffenberg, 1963, 1974 and Bramble, 1971 (Testudinidae). I have treated *Emydoidea* independently of *Deirochelys* as a result of reading Bramble's convincing 1974 analysis of emydid shell kinesis. Generic names are as in Conant, 1975. I have followed Bramble (1971) in using the name *Hesperotestudo* (Williams, 1950b) for the extinct North American tortoises (*Geochelone* of recent authors).

Each entry is divided into three sections. Section A applies to characters of the shell as a whole; sections B and C refer to features discernible on individual carapacial and plastral bones, respectively. The terminology is that of Zangerl (1969). The term "scute" is used for epidermal scale. The terms "seam" and "sulcus" are used interchangeably for scute impressions. All dimensions are in millimeters.

- 1A. Carapace composed of nuchal, neurals and pleurals only. Plastron not suturally united to carapace. No epidermal scute markings present.
- Carapace bones with sculptured pattern of ridges and pits. Striate ribs extend from expanded portions of costals.
- 1C. Only unpaired bone of plastron is boomerang-shaped fused epiplastron. Paired, sliver-like preplastra. Hyo-, hypo-, and xiphiplastra are plates of bone with sculptured callosities and rib-like projecting processes. Family *Trionychidae*, genus *Trionyx*, soft-shelled turtles ...5
- 1'A. Carapace with 10 or 11 pairs of peripheral bones. Plastron forms bridge with carapace. Sulcus-depressions of scutes usually visible.
- 1'B. Costals with projecting distal ribs do not have sculptured pattern of ridges and pits.
- 2A. Plastron much reduced in extent compared to carapace and joined through narrow bridge. Bone surface texture finely striate, slightly reminiscent of bird bone. Plastral bone, especially, tends to fracture in splintery fashion.
- 2B. Nuchal expanded laterally into "costiform" processes; wing-shaped (Fig. 4b). Costals with stout, projecting rib ends distally; peripherals with corresponding large, deep pits. No sulcus marks on peripherals.
- 2C. Entoplastron T-shaped. Bridge portion of hyo- and hypoplastra much reduced. Family Chelydridae,

- 2'B. Nuchal not expanded laterally. Costals with very short or no projecting rib ends in adults. Peripherals with evident scute marks and relatively small rib pits.
- 3A. Small shells (carapace length less than 150) with 10 pairs of peripheral bones.
- 3B. Marginal scutes (except possibly 9th and 10th) occupying less than ½ dorso-ventral dimension of peripherals (Fig. 5d). Peripherals flat. Strong curvature evident in costals.
- 3'A. Adults mostly larger than 150 carapace length (if small, entoplastron present usually showing humeropectoral sulcus). 11 pairs of peripheral bones.
- 3'B. Marginal scutes occupy more than 1/2 radial dimen-

sion of peripheral bone or coincide with costoperipheral suture. Peripherals usually slightly or strongly flared. Costals frequently not strongly curved.

- 3'C. Entoplastron present. Hyo- and hypoplastra elongate and squarish when complete. Pectoral scute wide or narrow but four-sided. Xiphiplastra usually tapering from broad anterior edge. Epiplastra firmly sutured to hypoplastra. Gular scutes present and large4
- 4A. Shells frequently large (carapace length greater than 500) and thick (greater than 10). If smaller, usually thick and rugose or thin with strongly-raised growth rings. If large and thin-shelled, margin of carapace and plastron thickened.
- 4B. Individual bones or fragments massive or, if thin, seemingly of light density and faintly striate. Peripherals always thick near margin. 12th marginal scutes united into single supracaudal so pygal usually without sulcus mark. Pleuromarginal sulcus usually overlies costoperipheral suture so sulcus mark not visible. (Large peripherals displaying notching of the posterior carapacial border or with prominent rib pits are *Macroclemys.*) Costal bones frequently wedge-shaped instead of parallel-sided. 2nd –5th neurals differentiated into alternating octangonal and quadrangular shapes. Rib-like processes may arise from peripherals (Fig. 10).
- 4'A. Shells always less than 500 carapace length (usually smaller). Thickness of peripheral border and plastron generally never exceeds 10. Growth rings not more than 2 mm deep.
- 4'B. Paired 12th marginal scutes present; interscute sulcus on pygal. Pleuromarginal sulcus marks usually on peripheral bones. Costals parallel-sided. 2nd-5th neurals hexagonal. Rib-ends may extend from costals, never from peripherals.
- 5(C). Epiplastral callosity extends over most of bone. Angle of epiplastron greater than 90°. Lateral projections of hyo- and hypoplastra make angles close to 45° and 40° with hypoplastral suture, respectively. Length of medial segment of xiphiplastron divided by length of posterolateral segment about 0.5. Trionyx muticus.
- 5'(C). Epiplastral callosity restricted to medial portion of bone. Angle of epiplastron about 90°. Lateral projections of hyo- and hypoplastra make angles close to 32° and 20°

- 6B. 1st vertebral narrow (Fig. 4a). No elevated marginal scutes.
- 6'B. 1st vertebral wide (Fig. 4c). 9th and 10th marginals may be elevated (expanded dorsally).
- 7(B). 9th and 10th marginals elevated dorsally, occupying most of peripheral surface. *Kinosternon flavescens*. p.27
- 7'(B). 9th and 10th marginals not elevated. Kinosternon subrubrum or bauri.
- 8(B). Neurals and costals keeled. Costals may show sulcus marks of supramarginal scutes. Posterior peripherals deeply double-notched (*i.e.*, at and between interperipheral sutures); longer radially than circumferentially. *Macroclemys temmincki*.
- 8'(B). Neurals and costals smooth. No supramarginal scutes. Posterior peripherals shallowly notched and longer circumferentially than radially. *Chelydra serpentina*. p.28

- 10A,B. Carapace smooth and unkeeled (C. guttata), sculptured and keeled (C. insculpta), or "in between" (C. muhlenbergi). 1st and 2nd suprapygals present. Lateral seams of 1st vertebral scute do not contact nuchal. Shelf on posterior peripherals.
- 10C. Position of humeropectoral sulcus well forward on entoplastron. No plastral hinge; plastron suturally united to carapace. Xiphiplastron deeply excavated. Genus Clemmys.
- 10'A,B. Carapace smooth or somewhat keeled or "bumpy". 8th neural usually fused to 1st suprapygal or latter absent. Lateral sulci of 1st vertebral may contact nuchal. Posterior peripherals may have shelf.
- 10'C. Humeropectoral sulcus on or immediately posterior to entoplastron. Hinge between hyo- and hypoplastra.

- 11B. Neurals 2-4 wider than long. 1st vertebral scute unconstricted; lateral seams not contacting nuchal (Fig. 4e). Seam between 1st vertebral and 1st pleural contacts 2nd marginal scute. Rib heads long; distance from central end of costal to rib attachment point more than 10% of costal width. 2nd and 3rd interpleural seams typically contact 7th and 9th marginals posterior to their midpoints. Distinct shelf formed by thickened parts of peripherals.
- 11C. Entoplastron roughly oval; longer than wide. Humeropectoral seam at posterior edge of entoplastron (usually not visible on entoplastron). Attachment areas of external abdominal oblique muscle deeply excavated in xiphiplastron. *Emydoidea blandingi* p. 30
- 11'B. Neurals 2-4 squarish or longer than wide. 1st vertebral constricted; lateral seams contact nuchal. Seam between 1st vertebral and 1st pleural contacts first marginal scute. Rib heads short; distance from central end of costal to rib attachment 10% or less of costal width. 2nd and 3rd interpleural seams contact 7th and 9th marginals at or anterior to their midpoints. Shelf inside rear margin of carapace formed between peripherals and costals.
- 11'C. Entoplastron subcircular. Humeropectoral seam well forward on entoplastron. Xiphiplastron shallowly or moderately excavated. Genus *Terrapene*12
- 12A. Shell high and rounded in lateral outline, somewhat elongate viewed dorsally and frequently large (150-300). Highest point posterior to hinge. Nuchal steeply rising. Hinge opposite 5th marginal scute. In most adult fossil and recent shells, bones are co-ossified frequently to the point of obliterating suture lines.
- 12B. Nuchal somewhat concave in lateral aspect. Neurals 2-6 usually keeled medially. Peripherals flared outward, sometimes keeled along bridge, but not emarginate (*i.e.*, outlining a slightly scalloped carapacial margin) in full-grown specimens. First marginal scute usually rectangular. Axillary scute usually present on 4th or overlapping 4th and 5th peripherals.
- 12'A. Shell low and relatively flat-topped in lateral aspect, subcircular in outline viewed dorsally. Maximum carapace length 180. Highest point above or anterior to hinge. Nuchal gently sloping rather than steeply rising. Hinge opposite seam between 5th and 6th marginal scutes. Individual shell bones separable at sutures; suture lines not obliterated.
- 12'B. Nuchal flat in lateral view. Median keel, if present, only on neurals 6-8. Peripherals normally not flaring outward, usually smooth along bridge but outlining a more-or-less scalloped margin, especially posterior to the bridge. 1st marginal scute usually irregularly oval or

triangular. Axillary scute rarely present but, if so, on 5th peripheral.

- Carapace with median keel or knobs (on neurals 3, 5, 8) or concentric ridges centered in scute areas.
- 13B. Nuchal with anterior excavation or notch (Fig. 4h); smooth. Carapacial bones smooth or with impressions of concentric growth rings. In genus *Graptemys* nuchal may be arched, forming dihedral angle with median, anteroposterior apex; posterior peripherals project horizontally; pygal inversely tapered and frequently elevated medially (character shared by *Chrysemys idahoensis*). 3rd interpleural seam terminates anterior to 9th peripheral.
- 13C. Plastron not expanded posteriorly; xiphiplastron constricted at femoroanal seam. Epiplastral lip not strongly expanded or thickened; epiplastral symphysis length (Fig. 9a) and plastral scute overlap small. Humeropectoral sulcus well behind entoplastron14
- 13'A. Carapace without strong median keel or knobs. Concentric ridges not centered in scute areas.
- 13'B. Nuchal not strongly excavated; smooth or vermiculately or coarsely sculptured. Carapace bones smooth or with moderate sculpturing. Nuchal not arched. Third interpleural seam terminates on 9th peripheral or at anterior suture of 9th peripheral (or at costoperipheral suture). Posterior peripherals project horizontally or ventrally; pygal tapered or parallel-sided, not elevated medially (except in *Chrysemys idahoensis*).
- 13'C. Plastron frequently expanded laterally posterior to bridge. Femoroanal constriction present or absent. Except in *Deirochelys*, epiplastral lip expanded or thickened; epiplastral symphysis length (Fig. 9a) and plastral scute overlap correspondingly long. Humeropectoral sulcus usually behind entoplastron.....16
- 14(B). Posterior peripheral border smooth. Peripherals sutured to costals in adults. 1st vertebral unconstricted anteriorly. *Malaclemys terrapin*, diamond-backs.
- 15A,C. Shell depressed posteriorly, resulting in low angle of ascent of bridge portion of hypoplastron.
- 15'A,C. Shell not depressed posteriorly; steeper angle (in transverse section) between ventral and bridge portions of hypoplastron.

- 16A. Carapace frequently finely and vermiculately sculptured, not keeled or knobbed.
- 16B. Neurals 2-5 wider than long. Seam between 1st vertebral and 1st pleural contacts second marginal scute. Rib heads long. *Deirochelys reticularia*.
- 16'A. Carapace usually smooth or coarsely sculptured, or moderately keeled. Not finely and vermiculately sculptured except in *rubriventris* section of subgenus *Pseudemys*.
- 17A. Carapace smooth or with fine vermiculate sculpturing; without keel. Posterior peripherals project horizontally or obliquely downward.
- 17B. Pygal usually inversely tapered. Posterior peripheral border smooth or notched only at distal ends of intermarginal seams. 1st vertebral strongly constricted anteriorly. 2nd marginal scute frequently partially overlies nuchal. Nuchal smooth, not dentate or strongly notched at anterior corners of cervical scute.
- 17'A. Carapace smooth or with longitudinal wrinkles and/or coarsely sculptured. Posterior peripherals project ventrally. Low median keel may be present.
- 17'B. Posterior peripheral border smooth or notched at distal ends of intermarginal seams and interperipheral sutures. 1st vertebral strongly constricted or only so that lateral seams of 1st vertebral barely encroach on lateral corners of nuchal. 2nd marginal does not contact nuchal. Nuchal smooth or with coarse sculpturing, dentate or strongly notched at anterior corners of cervical scute.
- 17'C. Anal notch absent or very shallow; xiphiplastron constricted or entire at femoroanal seam. Epiplastral lip strongly developed. Plastron expanded posteriorly . 19
- 18A,B. Vermiculate sculpturing of carapace and plastron often present. Nuchal notch or anterior excavation of carapace absent or not pronounced. Posterior peripheral border smooth; posterior peripherals and pygal project ventrally.
- 18'A,B. Carapace smooth or with weak longitudinal wrinkles on costals. Nuchal notch or anterior excavation of

carapace absent in Florida *floridana* – present to some degree in other races. Posterior peripheral border faintly or strongly notched at vertices of intermarginal seams; posterior peripherals and pygal project horizontally or obliquely downward.

- 19A. Carapace with low median keel, frequently rugose in adults.
- 19B. Posterior peripherals strongly notched at apices of intermarginal seams and interperipheral sutures. 1st vertebral scute strongly constricted anteriorly; nuchal notch or anterior excavation of carapace present. Nuchal rugose in mature specimens (at least in area of 1st pleural scute), dentate or notched at corners of cervical scute and forming an angle in lateral profile.
- 19'A. Carapace smooth or with longitudinal wrinkles on costals; without keel.
- 19'B. Posterior peripheral border entire. 1st vertebral constricted only to extent of barely encroaching on lateral corners of nuchal (Fig. 4g). Anterior excavation of carapace absent. Nuchal smooth, dentate (usually) at margin of cervical scute and flat in lateral profile.
- 20A. Maximum size very large (carapace length greater than 1000). Very little dermal armor. Surface texture of shell bone finely porous in appearance under some circumstances of mineralization and characteristically finely striate. Fractured shell bone reveals compact, non-cellular internal structure, at least in thin areas of the shell. Seam impressions wide, shallow, and bounded by gently raised, rounded ridges.
- 20B. Neurals and costals extremely thin (thickness 8 or less). Peripheral border inflated but peripherals thin at proximal sutures. Cervical scute wider than long; vertebral scutes wide. Anterior peripheral bones short. Pleurals may be tapered in alternate fashion (wedged). Nuchal generally not excavated; may be protrudent. Inguinal scute small, triangular, restricted to inguinal notch; may be divided.
- 20C. Pectoral scute relatively long (medial length greater than 20% interabdominal length). Strong gular projection sometimes present. Seam of 4th marginal crosses onto hypolastron. Nearly vertical lateral wall of xiphiplastral

excavation. Entoplastron not remarkably wider than long; interclavicular keel present on dorsal surface (Bramble, 1971). *Gopherus* sp., gopher tortoises . . p.38

- 20'A. Maximum size very large or small (carapace length less than 300). Dermal armor "excessive". Dense, amorphous surface texture of shell bone; cellular internal structure. Seam impressions deep, relatively narrow and without obvious boundary of raised ridges.
- 20'B. Carapace bones not disproportionately thin in large specimens – tending to be conspicuously thick in small forms. Cervical scute longer than wide; vertebrals not unusually wide. Anterior peripheral bones

tend to be elongated (radially). Pleural differentiation (wedging) usually not pronounced. Anterior margin of carapace tends to be excavated. Inguinal scute large, in broad contact with femoral.

20'C. Pectoral scute very short in large forms (less than 20% of interabdominal length). Strong gular projection always present; particularly in small forms. Seam of 4th marginal does not cross suture of 3rd peripheral onto hyoplastron. Lateral wall of xiphiplastral excavation rounded. Entoplastron frequently much wider than long; interclavicular keel not strongly developed. Genus Hesperotestudo, extinct tortoises p.40

APPENDIX B

Recent specimens of Chrysemys (Pseudemys) and Graptemys examined

Data for Figure 9 were obtained from the following specimens. Chrysemys f. floridana, f. penninsularis or intergrades: UMMZ S69, S458, S459, S783, S784, S786, S788, S1685, S2528, S2529, 130081, 129372, no number, MSU 3183. C. concinna suwanniensis: UMMZ S2530, S2531, 127058, MSU 518. C. concinna heiroglyphica and C. c. heiroglyphica x C. floridana hoyi: UMMZ S2896, 128176, 133875 (skeletal); 86665, 90123, 92730, 99229, 101754, 114040 (alcoholic). C. concinna texana x C. floridana hoyi: UT 2372, 2564, UMMZ 85087, 133836, WTA 652. Chrysemys rubriventris and nelsoni: UMMZ S449, S2527, S2533, 127059, 127060, MSU 474, 494. Graptemys geographica: UMMZ S64, S66, S67, S70, S118, S446, S464, S465, S467, S483, S486, 127062, 127063, 129783, UM R1673, R1674. *G. pseudogeographica* or *kohni*: UMMZ S445, S456, S457, S460, S484, no number, UM R1675.

Additional data for Table 3 came from these specimens. Chrysemys f. floridana: UM R1670. C. concinna suwanniensis: UM R1671, R1672. Chrysemys ornata: UMMZ S898, S1219, S1757, S1839, S2079, S2080, S2532.

Comparison of Chrysemys hibbardi was also made with UMMZ 129385, AMNH 64115, 75640 (C. c. suwanniensis), AMNH 75649 (C. c. concinna) AMNH 7014, 64156, 75641, 75644 (C. floridana ssp.), AMNH 75182 (Graptemys kohni), and large series of stuffed C. floridana and C. concinna at the NMNH Division of Reptiles and Amphibians.

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